

Climate, Tectonics or ...?: Speculations on the Recent Paleolimnology of Yellowstone Lake

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Abstract

The sediments of Yellowstone Lake may reveal the paleoecological history of this lake over the last few centuries. These sediments contain up to 60% biogenic silica derived from diatom frustules settling out from the overlying water. The sediment record reveals large variations in the diatom deposition over the last ~350 years. Some of these variations appear to correlate extremely well with independent climate records, particularly mean annual winter temperature and precipitation, derived from tree ring data extrapolations. A strong correlation occurs, for example, during an extended period of below-normal winter temperatures and above-normal precipitation seen during the late 1800s. Below-normal winter temperatures can significantly extend winter ice cover and shorten the ice-free, isothermal period during which the spring diatom bloom occurs. Rapid thermal stratification following prolonged ice cover may reduce annual diatom production and the subsequent silica deposition. Yet the forcing factors in this system may not be so straightforward. Sublacustrine hydrothermal springs found in the lake are a potential source of nutrients that may vary in strength and in time. These inputs may have the potential to alter the nutrient biogeochemistry of the lake. A pronounced chloride enrichment observed within the lake may be explained by input of a source of undiluted geothermal water equivalent to >0.06% of the riverine input. Calculations based upon silica removal indicate that such hydrothermal inputs would have to contribute up to $\sim 10^7$ moles of nitrogen annually, for example, in order to significantly shift the nutrient status of the lake. Observations to date, which are limited in space and time, do not appear to support such a flux for the whole lake. However, the existence of high-activity vents in past eras (as indicated by numerous relict features) or in unexplored regions of the lake cannot be ruled out.

Introduction

The integrity and value of the paleoecological history recorded in lake sediments is dependent upon a number of factors. For example, a good record contains: a relatively undisturbed sediment accumulation rate regime, a coherent and quantifiable sediment chronology, and minimal or quantifiable post-depositional alteration of biological or geochemical indicators as a consequence of diagenesis, mixing, migration, or other physical disturbances. The time scale of interest

can range from years to millennia and is dependent upon the age of the lake and the existence of geochronological techniques to independently date various sediment horizons within the sediment column. Sediments within the depositional basins of Yellowstone Lake consist largely of a diatom ooze, up to 60% biogenic silica by weight, and have been examined in a number of studies for their potential in revealing the ecological history of this high-altitude system. Shero and Parker (1976) examined sediments from the South and Southeast arms of the lake and identified over 150 taxa of diatoms in cores with maximum ages estimated to be on the order of 1500 BP (years before the present). Many of these taxa were extremely rare, but the diversity of the flora indicates a potentially rich record of ecological changes and evolution over this period. In general, Shero and Parker (1976) observed a decrease in diatom abundance over the last 1500 years and hypothesized that lake productivity may have decreased over that period as a consequence of decreases in the annual nutrient supply, perhaps related to decreases in annual precipitation. More recently, Kilham et al. (1996) have provided an excellent review of the factors linking diatoms and climate change in the large lakes of the Yellowstone ecosystem.

The observations reported here are the result of work begun by our group some time ago (1983) in looking at the recent record (i.e., over the last 200 years) in these sediments, and in the sublacustrine hydrogeothermal activity within the Yellowstone Lake basin (Klump et al 1988).

Analytical Methods

Sediment cores were collected using a standard 7.5-cm-diameter Benthos gravity corer deployed from the U.S. Fish and Wildlife Service *R/V Cutthroat*. Intact cores in excess of 60 cm in length were retrieved. Upon returning to shore, cores were sectioned on a hydraulic extruder at 0.5- to 5-cm intervals. Sediment sections were placed in tared plastic 125-ml bottles, dried in an oven at 60°C to a constant weight, and reweighed to determine the percent water content and porosity, assuming a dry sediment density of 2.3 g cm⁻³. Sediments were pulverized in a mortar and pestle to a fine powder. Pb-210 activities were determined following a modification of the procedure of Robbins and Edgington (1975). An internal Po-208 standard was added to ~0.5 g of sediment to determine recovery efficiency, and the sediments were digested in 6N HCl at 95°C with sequential additions of 30% hydrogen peroxide. The solutions were cooled, filtered, pH-adjusted to 0.5 to 1.0, and amended with 100 mg of ascorbic acid. Po-210 and Po-208 were plated onto a polished copper disk in a boiling water bath and counted via low-level alpha spectrometry.

Pigments (chlorophyll and total carotenoids) were measured according to the spectrophotometric technique given by Strickland and Parsons (1972). Aliquots of whole, wet sediments were extracted in 90% acetone at approximately 30 ml per gram dry sediment for >20 hours in the dark, centrifuged, and the supernatant decanted into a 5-cm-path-length spectrophotometer cell. Values for carotenoids are reported as relative concentrations for time-series analysis and are roughly equivalent to ug g⁻¹ dry sed. *Daphnia* winter-resting eggs or ephippia were count-

ed in known wet-sediment aliquots under a dissecting microscope and are reported as number per gram dry sediment. Ehippia were easily recognized and counted, being the only large particles in these otherwise very fine-grained sediments. Biogenic silica was determined following the differential dissolution technique of DeMaster (1981) in which sediments are dissolved in a 85°C, 1% solution of Na_2CO_3 . Sequential samples of the solution are analyzed for dissolved silica (Strickland and Parsons 1972) over a 5-hour period and the initial rapid rise in silica concentration taken as the dissolution of diatom frustules. Scanning electron microscopy micrographs made of both dissolved and untreated samples confirmed complete dissolution.

Results and Discussion

The cores examined here were collected from the deepest portion of the central basin of West Thumb in 1983 and 1985. The water depth here is ~310 feet and was, at the time, considered to be the deepest sounding in the lake. (Subsequently, more precise bathymetry with higher spatial resolution and remotely operated vehicle explorations of the bottom shifted the known deepest location to a small “canyon” southeast of Stevenson Island with soundings of nearly 400 feet.) Visually, the cores appeared to be relatively undisturbed, with a surface “flocculent layer” of a few millimeters. Below this surface floc, sediments were consolidated, highly porous (90% at 50 cm), fine-grained muds. X-radiographs revealed some apparent laminations, although not distinct or regular. In casual observations at the time of collection, benthic macroinvertebrate infauna were not observed and biogenic mixing is assumed to be minimal. The Pb-210 geochronology at this location for these cores (see Figure 1 for 1985) appears to bear this observation out. Excess Pb-210 (half-life 22.3 years) decreases exponentially from a value of ~23 pCi g^{-1} at the sediment–water interface to a supported value of <0.3 pCi g^{-1} at a depth of ~18 cm. Calculations from a curve fit of the excess Pb-210 data to the mass sediment accumulated with depth (g cm^{-2}) yield a net average mass sediment accumulation rate over this interval of ~22 $\text{mg cm}^{-2} \text{y}^{-1}$ ($r^2 = 0.97$), or a linear sedimentation rate of ~0.16 cm y^{-1} . In general, Pb-210 dating may be extended to ~5 half-lives, or 100–120 BP. In this analysis we have extrapolated this rate to the length of core for chronological purposes, but add the caveat that dates prior to about 1870 are simple extrapolations and that these dates become increasingly sensitive to relatively small changes in sedimentation rate with increasing age. Indeed, one of the most interesting features in this core dates near the lower end for resolution by Pb-210 (1860–1900). This extrapolation, however, does fall within the range of sedimentation rates calculated by Shuey et al (1977) using paleomagnetic data of 0.100 to 0.213 cm y^{-1} (excluding the South Arm) for the period 1175 AD to present.

Diatom remains (intact frustules and fragments) make up the major portion of the sediment mass in the depositional basin of West Thumb. The biogenic silica content of these sediments reaches nearly 60% by weight at depth, but ranges from ~45% to 58% over the last 200 years (Figure 2). These changes in the biogenic silica content argue for significant changes in the production, burial, or

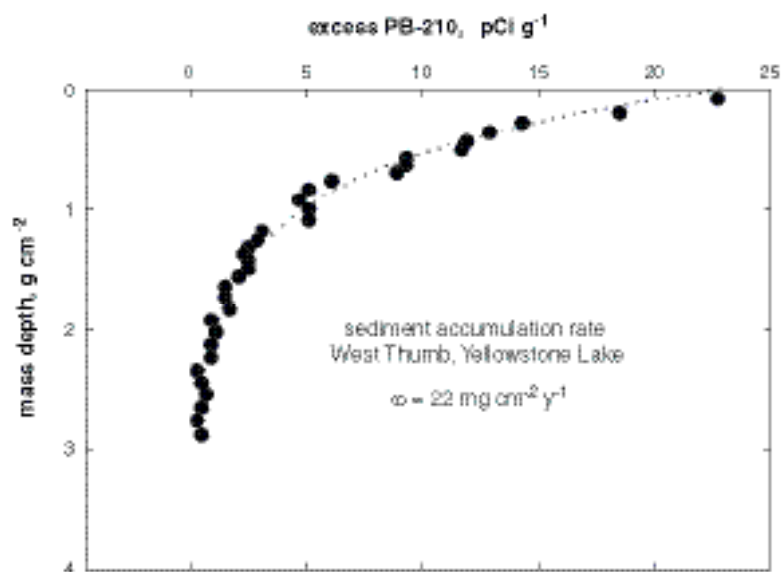


Figure 1. The Pb-210 geochronology for the West Thumb core (WT-85) shows a remarkably constant mass sedimentation rate averaging $\sim 22 \text{ mg cm}^{-2} \text{ y}^{-1}$.

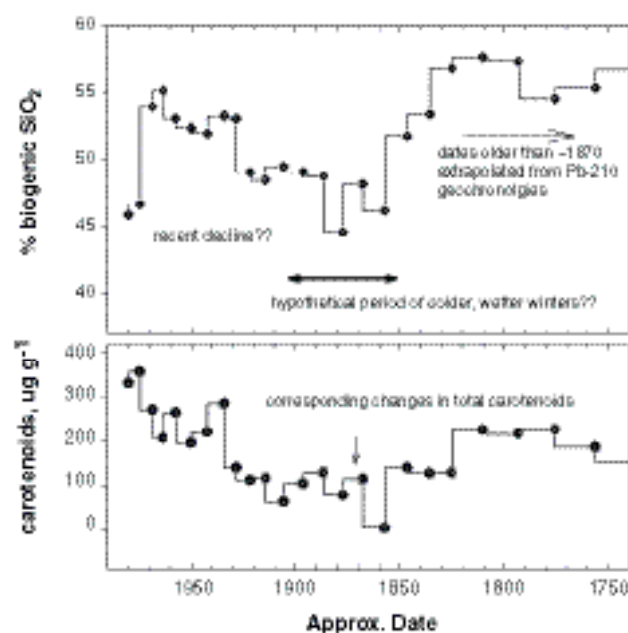


Figure 2. Percent biogenic silica (dry weight) and total carotenoids plotted as a function of time of deposition in WT-83. Both show significant drops in the late 1800s.

preservation of diatoms over time. Nothing within these cores indicates an alteration in the preservation of diatoms, although significant changes in speciation to species with more fragile, readily dissolved frustules is possible. Sedimentation rates, on the other hand, are remarkably constant. Our hypothesis is that the changes observed in the biogenic silica record are the result of changes in diatom production related to annual variations in whole lake productivity.

Of particular interest is the dramatic decrease in biogenic silica production (i.e., burial) in the late 1800s. At steady state, this decrease would translate to a drop in diatom production of 10–20%, depending on the reference period. The core used for this analysis was collected in 1983 and was sectioned at 1-cm intervals to a depth of 20 cm, 2-cm intervals to a depth of 30 cm, and then at 5-cm intervals to the bottom of the core. The lowest point in the biogenic silica stratigraphy (44.6%) occurs at 14–15 cm, an interval for which we place a date of ca. 1877. Quantification of simple algal pigments preserved in this record also shows a strong correlation with the diatom record, and carotenoids track biogenic silica content extremely well (Figure 2).

A principal goal of paleolimnology is, of course, to use such biotic tracers to decipher past conditions in the lake, in an attempt to determine how planktonic communities and the ecology of the system have responded to changes in climate, ecosystem structure, evolutionary pressure, and both naturally occurring (e.g., forest fires) and anthropogenic (e.g., watershed development) processes (e.g., Meyer et al. 1992; Kilham et al. 1996). In Yellowstone Lake, all of these types of processes are potential contributors to changing lake ecology.

Climate Changes

Temperate lakes, and perhaps high-altitude lakes in particular, are especially susceptible to changes in climate. One of the principal reasons for this is the annual physical cycle of most temperate lakes, which is driven by the annual temperature oscillation. A high-altitude lake in one of the coldest regions of the U.S., Yellowstone is ice covered for nearly six months of the year. Inter-annual changes in the temperature climate can vary the temporal extent of ice cover and of stratified and unstratified periods by several weeks or even longer. The ice free season begins with an isothermal, well mixed water column in the spring. As solar heating increases the lake shifts to a thermally stratified, stable water column in the summer, followed by overturn and mixing upon cooling again in the fall.

Determination of a climate signal in lake sediments is confounded by the variety of potential forcing functions. Correlations with other climate records, however, may be useful. Using the analysis of tree ring data, Douglas and Stockton (1975) reconstructed a long term seasonal temperature and precipitation record for the Yellowstone National Park region. This reconstruction dates back to 1750 with both seasonal and annual coverage. Of interest here is their reconstruction for winter temperatures and precipitation (Figure 3). A simple examination of this record shows what appears to be an anomalous period during the late 1800s. Prior to about 1860 and after about 1905, this record shows predicted winter tem-

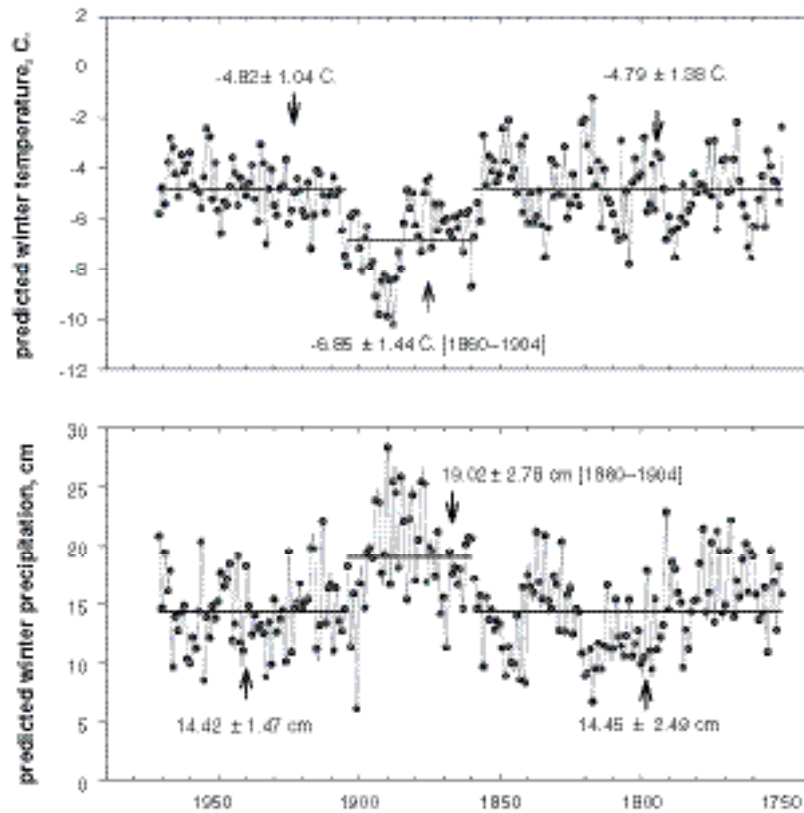


Figure 3. Paleoclimate predictions for winter (November-March) temperatures and pre -
 cipitation in Yellowstone based upon tree ring climate reconstructions (from Douglas and
 Stockton 1974). Both below-average temperatures and above-average precipitation are
 predicted for the late 1800s, particularly during the period 1885–1894 when temperatures
 were nearly 4°C lower and precipitation 8 cm higher than “normal” conditions prior to
 1860 and after 1905.

peratures to vary about a remarkably constant mean value of $\sim 4.8^{\circ} \pm 1.4^{\circ}\text{C}$. Predicted winter precipitation likewise varies about a relatively constant mean of $\sim 14.4 \pm 2.5$ cm for these two long periods. During the late 1800s, however, there is a significant drop in predicted temperatures by at least 2°C , to a mean of $-6.85^{\circ} \pm 1.4^{\circ}\text{C}$, concomitant with a significant increase in predicted winter precipitation by at least 4.5 cm, to 19.0 ± 2.8 cm. Assuming this is snow cover, this would be equivalent to ~ 45 cm of additional snowfall. Both of these would appear to be, in this region, significant climate variations. In fact, a closer examination of the data for 1860–1905 shows that for shorter periods of 10 to 20 years, the departures from the long-term means are even greater. For example, for the period 1885–1894, the average predicted winter temperature is $-8.81^{\circ} \pm 0.89^{\circ}\text{C}$, 4°C below “normal,” and the average predicted winter precipitation is 22.34 ± 3.88 cm, nearly 8 cm above “normal.” The combined effect of colder-than-nor-

mal temperatures and above-average snowfall could easily extend the ice-cover period on Yellowstone Lake by weeks. Typically, ice-out occurs in late May or early June. Prolonging ice cover, even by two or three weeks, could have dramatic effects on lake ecology. Results from regional climate models for the impact CO₂ doubling on the thermal regime of Yellowstone Lake are indicative of the sensitivity of the lake to climatic-scale temperature changes. For example, the average annual surface temperature is increased by 1.6°C for a 2xCO₂ scenario (Hostetler and Giorgi 1995). This warming reduces the annual duration of ice cover by over six weeks, from 196 days to 152 days.

Primary production during the spring bloom is particularly important in deep lakes such as Yellowstone. During the spring transitional period, the lake is isothermal and well mixed. Because of mixing, algae throughout the water column may be exposed to light and have sufficient nutrients to sustain rapid growth. Once the lake warms, however, and begins to stratify, hypolimnetic nutrients are largely out of the reach of the photic zone and photosynthetic primary production is limited to the fairly shallow region of the epilimnion where nutrients, no longer being replenished from deeper waters, can be rapidly depleted. The spring bloom is triggered, in general, by light. Prolonged ice cover may have multiple effects. First, it insulates the water column from solar radiation, limiting algal growth, and secondly, it contracts the length of the isothermal spring bloom period. In the latter case, by the time ice-out occurs, solar heat inputs may be near their maximum and the lake can stratify very quickly, perhaps in a matter of days. The result: there is little time to extract stored hypolimnetic nutrients before they are “sealed off” by the rapidly forming thermocline, and the productivity of the spring bloom is significantly limited. Similar climatic-forcing effects have been observed as a consequence of El Niño events in Castle Lake, a temperate, subalpine lake in California. Year-to-year changes in the amount of snowfall from February through April, which determine the date of ice thawing (by up to more than one month later in the spring), coupled with early heating and stratification, resulted in significant interannual variations in heat stored within the lake (Strub et al. 1985). This ranged from early thaws with extended mixing and high productivity, to late thaws with incomplete mixing, a failure to renew photic zone nutrients, and consequent low productivity. During 1983, for example, when the lake remained ice covered until 6 July, primary production during the summer was only 25% of normal. In a similar situation, interannual variations in zooplankton abundance (principally the herbivorous *Daphnia hyalina*) in Lake Windermere, United Kingdom, strongly correlated with the timing of thermal stratification (George and Harris 1985). Interestingly, zooplankton biomass was higher in cool years coinciding with the period of maximum food availability, whereas in warm years the preferred algal food species tended to appear earlier and may have been in decline by the time *Daphnia* begin to reproduce.

The paleo-record of zooplankton is much less robust in lakes. Cladocerans, however, are a major component of the zooplankton in Yellowstone Lake and the sediments contain abundant ephippia, or winter-resting eggs. Recently, there is

renewed interest in paleoecological studies using these resting eggs, including genetic and evolutionary histories (Hairston 1996). Here, however, we report only our observations on numbers deposited and preserved through time. Although this record is highly variable (Figure 4), it does appear that prior to about 1900 there are episodes of high and low ephippia production. One of the highest of these correlates to a date in the 1870s and 1880s, a period of low diatom production in the lake and cold, wetter winter weather. Three of the eight intervals in which numbers exceed 300 per g occur within this period. Coincidence, perhaps, but this observation may relate to spring bloom timing effects, low primary production, or changes in speciation. *Daphnia* stressed by low food resources, for example, may shunt more energy into egg production, resulting in greater ephippia abundance in years in which primary production is decreased. The clearest trend in the ephippia record, however, is the decline in numbers after about 1910. Speculations for the reason for this drop could include all of the above, as well changes in ecosystem dynamics, such as abundance shifts in planktivorous fish populations, an impact that can be triggered by the invasion of non-native species.

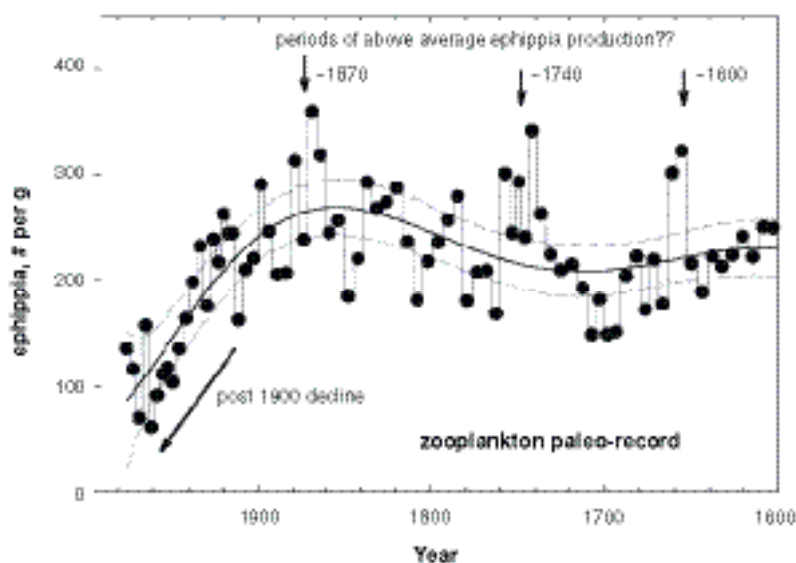


Figure 4. The abundance of ephippia (number per gram dry weight) in West Thumb sediments (WT-85) as a function of the year of deposition.

Geochemical Budgets and Geothermal Inputs

Its location within the Yellowstone caldera and over a geothermal hot spot makes Yellowstone Lake unique. Studies over the last 15 years have revealed a sublacustrine plumbing system made up of diverse underwater hot springs, fumaroles, and seeps (Klump et al. 1988). Could the geothermally enriched flu-

ids emanating from these features have the potential to “fertilize” the lake to a degree sufficient to alter primary production? How much would be required? One approach is to simply calculate backwards from the known diatom accumulation rates. For example, if we assume that significant deposition only occurs at depths greater than 40 m, then slightly more than 50% of the area of the lake is depositional. Further, if we assume that the sediment accumulation rate averaged over this area is $\sim 10 \text{ mg cm}^{-2} \text{ y}^{-1}$ (or roughly one-half of the $22 \text{ mg cm}^{-2} \text{ y}^{-1}$ measured in West Thumb), then the average biogenic silica removal rate (at 50% biogenic silica by weight in the sediment) for the whole lake is on the order of $2.5 \text{ mg (42 } \mu\text{mol) Si cm}^{-2} \text{ y}^{-1}$. The average depth of the lake is 42 m; hence, the average silica removal rate from lake water via burial is $\sim 10 \text{ } \mu\text{mol L}^{-1} \text{ y}^{-1}$. Silica concentrations in Yellowstone Lake average over $150 \text{ } \mu\text{mol L}^{-1}$. Hence, this rate of removal would hardly be detectable in lake water. Even if silica deposition were more widespread, e.g., at depths $>20 \text{ m}$ (i.e., 75% of the lake floor), and average sedimentation rates more rapid, e.g., $20 \text{ mg cm}^{-2} \text{ y}^{-1}$, then annual silica depletion would rise to $30 \text{ } \mu\text{mol L}^{-1} \text{ y}^{-1}$. Although the data are infrequent and variable, this number approaches the depletion we have observed between inflow and outflow concentrations in the Yellowstone River.

Since the volume of the lake is $\sim 1.4 \times 10^{10} \text{ m}^3$, a 20% change in diatom production (i.e., in burial) would likewise require a mass of diatom silica of $\sim 3 \times 10^7 \text{ mol Si y}^{-1}$. Since silica is not limiting in this system, changes in the flux of another micronutrient would have to be responsible for any hypothesized “fertilization” effect, i.e., changes in new nutrient inputs over time. Take, for example, nitrogen or phosphorus. Average stoichiometries for diatom production vary, but an approximate Si:N ratio of $\sim 1\text{--}2$ and Si:P ratio of $\sim 20\text{--}25$ are reasonable (Redfield ratios are 16:16:1). To produce $3 \times 10^7 \text{ mol Si y}^{-1}$ would therefore require roughly 10^7 moles of nitrogen and 10^6 moles of phosphorus. To date the *highest* dissolved inorganic nitrogen and phosphorus concentrations we have measured in vent fluids are ~ 100 and $30 \text{ } \mu\text{mol L}^{-1}$, respectively, measured in 1987–1989. Since that time the concentrations we have observed in vent fluids have been considerably more dilute. Thermal ponds on shore often have extremely high concentrations of inorganic nutrients. In Mary Bay, for example, we have measured dissolved ammonium concentrations in small ponds in excess of $600 \text{ } \mu\text{mol L}^{-1}$. Assuming vent waters contain inorganic nutrients at the high end of our measurements in the lake, the hydrothermal flux required to effect a 20% diatom productivity shift from changes in nutrient supply is on the order of $0.3\text{--}1 \times 10^8 \text{ m}^3 \text{ y}^{-1}$ or $\sim 2\%\text{--}7\%$ of the riverine inflow. Silicon itself is a major constituent in hydrothermal vent waters, being readily leached from volcanic rocks rich in silicon at high temperatures. We have measured dissolved silica concentrations as high as 3 mmol L^{-1} in waters emanating from shallow vents in Sedge Bay (Remsen et al. 1990).

Chloride is a conservative element highly enriched in geothermal waters, and its flux into surface waters has been used as an indication of fluctuations in regional geothermal activity (Norton and Freidman 1985). Comparison of average chloride concentrations in the major inflow ($<10 \text{ } \mu\text{mol L}^{-1}$) and outflow

(~150 $\mu\text{mol L}^{-1}$) shows that chloride is enriched by up to fifteenfold within the lake. Chloride concentrations in undiluted geothermal source waters in the park have been estimated to be as high as ~10–20 mmol L^{-1} (Truesdell et al. 1977; Fournier 1979). The highest we have measured in sublacustrine vents in the lake is ~3 mmol L^{-1} (Klump et al. 1992). At these levels it would require the addition of ~ 10^7 m^3 of vent water annually (~1% of river inflow) in order to raise the concentration in the Yellowstone River outflow by 140 $\mu\text{mol L}^{-1}$ (ignoring inputs from precipitation, which are assumed to be minor based upon low Cl^- levels in rainfall). If this flow were concentrated in 0.0001% of the lake bottom (i.e., 1,000 cm^2 of vents per 10 ha, which implies 3,500 such vents fields) the flow in these vents fields would need to average ~5 L min^{-1} . Our observations to date would seem to indicate that vents of this magnitude are not this numerous, but the task of accurately characterizing and quantifying activity at an areal frequency of only 1:100,000 is problematic.

The fact remains, however, that lake water is enriched in Cl^- , requiring a contribution of $1.7 \times 10^7 \text{ mol Cl}^-$ annually. This is equivalent to a ~0.06% contribution to the hydrologic budget from undiluted geothermal source waters (at 20 mmol L^{-1}). A variety of additional sources may be considered, e.g., surface runoff from contiguous geothermal areas in West Thumb, Mary Bay, Sedge Bay, Turbid Lake/Sedge Creek, and other areas; diffusion from geothermally enriched porewaters (see Aguilar et al., this volume); and wind-blown minerals or other dry deposition processes. Norton and Friedman (1985) estimate that 93% of the total chloride flux out of the park derives from hydrothermal sources, with the remainder divided among atmospheric inputs (2.7%), rock weathering (4%), and human contributions (0.2%).

It is apparent that geothermal activity varies over time. Whether this variability is sufficient to drive productivity shifts within Yellowstone Lake is still an open question, but our current observations, at least with respect to conventional nutrients, would seem to indicate that it is not. However, we still have explored only a very small fraction of the lake bottom. High-precision bathymetric charts being produced by the U.S. Geological Survey may help us answer these questions by assisting in pinpointing potentially active regions of the lake floor for further exploration. Furthermore, numerous sublacustrine vent field concretions, relict vent plumbing, and the meter-scale spires discovered in Bridge Bay (see Cuhel, Aguilar et al. this volume) are composed almost entirely (95%) of amorphous silica, indicating that very active, high-concentration vents have been common in the lake in the past. Hence, the potential for significant geothermally active episodes in the lake's history appears to be real.

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Investigating the Microbial Ecology of Yellowstone Lake

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Abstract

Yellowstone National Park is well known for its geothermal features. Among microbiologists it is equally well known for its unique microbial ecology and extreme habitats associated with terrestrial hot springs, geysers, and fumaroles. Yellowstone Lake has also been shown to contain geothermal activity, and the presence of hydrothermal vents with water temperatures up to 120°C have been reported. The vents emit a number of compounds which are important to microorganisms as nutrients for growth or substrates for energy. Thus, similar to the terrestrial habitats, Yellowstone Lake presents unique systems to assess microbial diversity and ecology. In order to examine the microbial ecology of the lake and its hydrothermal features, we have used both traditional culture and enrichment techniques to isolate bacteria, and modern molecular methods to assess the microbial diversity. For example, enrichment and cultural methods have yielded the characterization of a new genus and species of thermophilic sulfate-reducing bacteria, *Thermodesulfovibrio yellowstonii*, isolated from a hydrothermal vent in Sedge Bay.

Introduction

Microbial ecology is the study of microorganisms in relation to their biotic and abiotic environment. In practice, it has been described in a graduate student motto as “the study of physiology under the worst possible conditions” (Brock 1966). More recently, microbial ecology has also been indicated to be the link between all branches of microbiology (Zinder and Salyers 2001). In any case, similar to traditional ecology, microbial ecologists study individual organisms, populations (of individuals), communities (of populations), and ecosystems. This is done with a variety of approaches and tools, including microscopy, culturing, molecular biology, and biochemistry. Much of what is studied by microbial ecologists revolves around three questions: (1) Who is out there? (2) How many are there? and (3) What are they doing?

Yellowstone Lake has been considered to be oligotrophic (e.g., Remsen et al. 1990; Gresswell et al. 1994). In other words, it has a low amount of productivity and is nutrient-poor. However, recent reports have suggested that the levels of nutrients indicate it should be considered more mesotrophic, or have a higher level of productivity than previously believed (Kilham et al. 1996; Theriot et al. 1997). When applying the above questions to Yellowstone Lake, the task of answering them might appear to be somewhat daunting. The sheer size of the

lake makes it difficult to know just where a microbial ecologist should begin (Table 1). It gets even more complex if one considers that there are around a million bacteria per milliliter of water. In Yellowstone Lake, our focus has been on

Table 1. Characteristics of Yellowstone Lake. Data compiled from Pierce (1987), Kaeding et al. (1996), and Kilham et al. (1996).

Altitude above mean sea level	2,356.0 m
Surface area	341.0 km ²
Shore line length	239.0 km
Mean depth	48.5 m
Maximum depth	107.0 m
Estimated capacity	1.517 x 10 ¹³

the geothermal activity exhibited by sublacustrine (i.e., at the bottom of lakes) hydrothermal vents and geysers (Marocchi et al. 2001; Remsen et al., this volume). However, even considering these locations presents some difficulties. The water and gases emanating from vents and geysers have influences that can extend some distance away from their origin (Figure 1). Water coming out of a vent forms a plume which mixes with the bulk water and transports vent material throughout the water column. The influence and the size of the plume depends upon the amount and periodicity of flow coming out of the vent orifice. Gas bubbles from a vent adsorb microorganisms and carry them to the water surface, where, after the bubble bursts, bacteria can be deposited at the air–water interface on what are called *film drops*, or transported into the atmosphere on what are known as *jet drops* (Maki and Hermansson 1994). Solid objects, such as rocks or aquatic plants that intersect the plume or gas flow, can also develop microbial communities directly influenced by vent emanations. In addition, there are also influences on the sediments that surround the vent, starting at the tube leading to the vent orifice and extending outwards. Thus, to get a complete picture, a variety of factors must be examined.

The presence of the hydrothermal vents provides another factor to consider for a microbial ecologist: temperature. The lake contains a range of temperatures that extend into the extreme. The lake generally becomes stratified in July and the thermocline may exist through mid-September with surface temperatures very seldom going above 18°C (Gresswell et al. 1994; Kaeding et al. 1996). Ice cover occurs from mid-December through May or even June, providing plenty of low temperatures (e.g., <4°C). On the other end of the temperature range, the hydrothermal vents have waters that reach up to 120°C (Buchholz et al. 1995; Klump et al. 1995). This allows for the presence of the entire range of optimal-growth temperature categories of microorganisms (Table 2) in Yellowstone Lake. Some microbes in the domain *Eucarya* can grow up into the thermophilic range, but most have lower (mesophilic) temperature requirements. Of the procaryotes, members of the domain *Bacteria* are found in all categories. Procaryotes that fall into the hyperthermophile category belong primarily in the domain *Archaea* (Brock 1994).

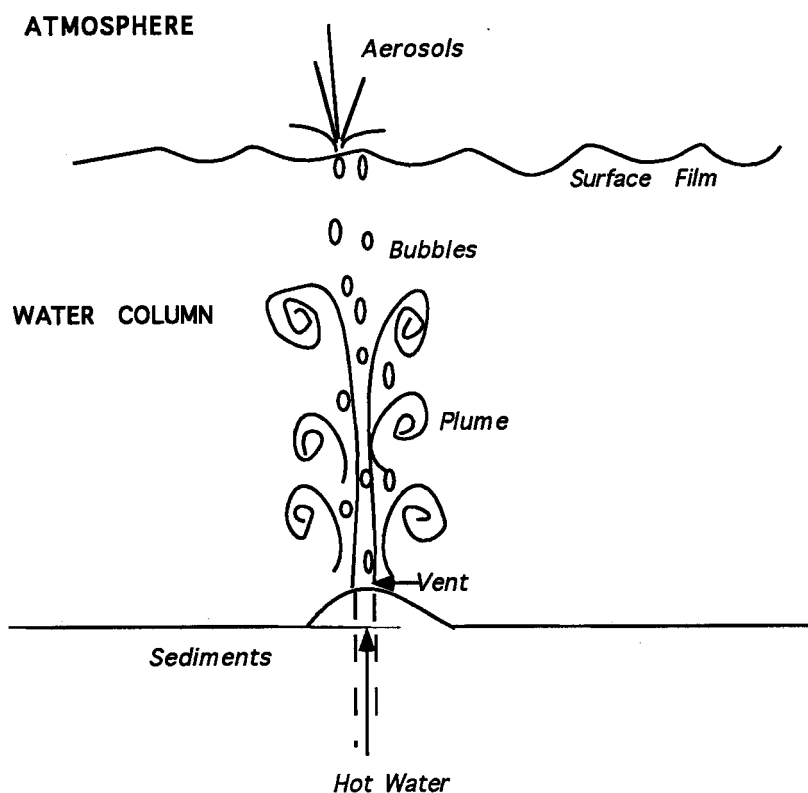


Figure 1. Schematic of the influence a hydrothermal vent may have on the water body into which it flows.

Table 2. Categories of growth temperature optima for microorganisms.

<i>Description</i>	<i>Growth temperature optima</i>
Hyperthermophiles	>80°C
Thermophiles	45-80°C
Mesophiles	15-45°C
Psychrophiles	<15°C

Of the three questions listed above, “What are they doing?” has been addressed elsewhere (Cuhel, Aguilar, Anderson et al., this volume), so the focus here will be on some of our work to determine “Who is out there?” and “How many are there?” in Yellowstone Lake. Our interest has been primarily on the procaryotic microorganisms of the domains *Bacteria* and *Archaea*, although it will be clear that our work did not exclude the *Eucarya*.

Sampling

Most of our collection of hydrothermal vent and bulk waters on the lake was accomplished using the National Park Service research vessel *Cutthroat*. Both SCUBA divers (in shallow waters) and a remotely operated vehicle (ROV; in deeper waters) have been used to collect the vent water samples (e.g., Klump et al. 1992; Buchholz et al. 1995). Over the years, we have been on a learning curve using the ROV; after each sampling season, discussions with Dave Loyalvo (Eastern Oceanics, West Redding, Connecticut), who operates the ROV for us in the lake, have resulted in modifications to enable better collection of water and other samples. Some idea of the changes involved have been presented elsewhere (Marocchi et al. 2001; Remsen et al., this volume) and will not be discussed in detail.

Who is Out There? How Many are There? Quantitative Analyses

Analysis of hydrothermal vent water chemistry reveals that not only are the vents in various regions of the lake different, but vents within the same region appear distinct from each other (Klump et al. 1988; Remsen et al. 1990; Klump et al. 1992; Buchholz et al. 1995). The chemistry data suggest that each of these vents could represent a different microbial habitat, and thus should have different microbial communities. Initially, some of our research examined these communities using quantitative methods.

We assessed microbial communities quantitatively by two means. First, we used multiple staining techniques and fluorescence microscopy to count microbial cells directly (e.g., Sherr and Sherr 1983). Second, we used culture methods where a water sample is serially diluted and each dilution is used to inoculate a solid growth medium that is incubated, and after a certain amount of time the colonies that arise (called *colony-forming units*, or CFU) are counted. In the latter case, the medium we have used is Castenholz TYE (Castenholz 1969) and is solidified using agar for mesophiles or Gelrite for thermophiles and hyperthermophiles (see Table 2 for temperature ranges involved). Using these methods to compare samples from different vents in Sedge Bay revealed that the numbers of distinct types of microorganisms determined by direct counts and CFU vary between vents and are different from those in the bulk waters (Figure 2). These data support the idea of each vent being able to maintain different microbial communities. Some types of microorganisms (e.g., phototrophs, algae excluding the cyanobacteria) were only visible in the bulk water samples. All other types were present in all samples examined. One important type of microbe present everywhere was the heteroflagellates. These are eucaryotic microorganisms that feed upon the bacteria and provide the beginning link from procaryotes to larger organisms in the food chain, eventually leading to zooplankton and fish.

However, the data presented in Figure 2 also illustrate the major problem associated with using only a culture approach for isolating bacteria and other microorganisms—or with examining any form of microbial diversity. As can be seen when comparing the number of bacterial CFU and the total counts of bacteria in the different vent samples, the number of CFU is around two orders of

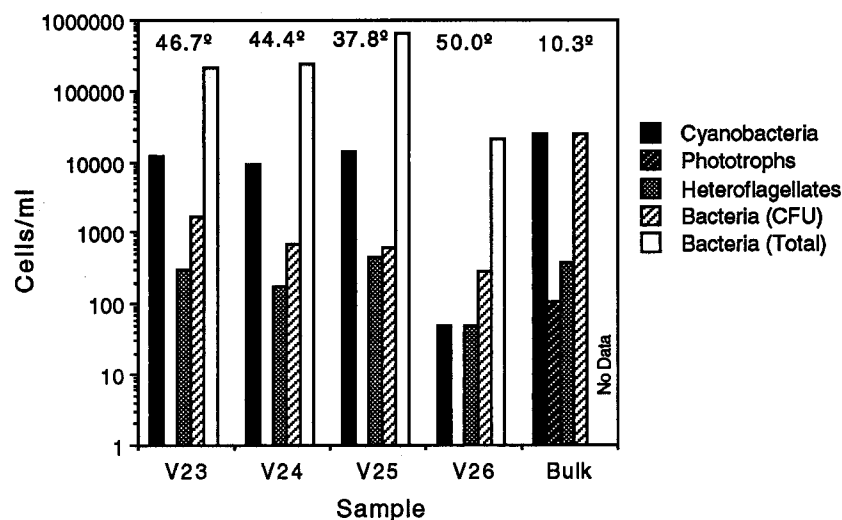


Figure 2. Comparison of the microbial communities of four separate hydrothermal vents in Sedge Bay. "V" followed by a number indicates the vent sampled while "Bulk" indicates a non-vent sample from the water column. Temperatures listed above each sample are in °C. No direct count data of bacteria in the bulk water sample were available.

magnitude less than (or ~1%) the total count. This is because using growth media of any type selects only for the organisms that can grow on that particular medium, and the vast majority of bacteria out there are unlikely to all grow on the same medium. This low ability to culture microorganisms extends to just about every habitat that has been studied and has inspired the use of molecular approaches for assessing microbial diversity and ecology. These molecular approaches allow the assessment of microbial diversity and identification of microorganisms without cultivation (e.g., Amann et al. 1995).

We have been using a combination of enrichment culture and molecular methods to assess the procaryotic microorganisms from both hydrothermal vent and bulk water samples (Figure 3). These include members of both the *Bacteria* and *Archaea*. On the enrichment side, we can focus on groups of microorganisms that grow under very specific conditions and utilize the chemistry of the hydrothermal vent emanations for growth or energy (e.g., Remsen et al. 1990). We can then isolate individual microorganisms and characterize and identify them. This was generally the methodology used by microbial ecologists everywhere before the advent of molecular techniques. Now, however, to identify and characterize a single type of bacterium not only are phenotypic attributes used (e.g., morphology, fine structure, growth substrates, conditions for growth, etc.), but so are genotypic characteristics determined through molecular techniques. These allow the investigator to get a clearer picture of the bacterium in question.

Molecular Analyses for Identification and Diversity

One of the genes most used to deduce the position of a bacterium phyloge-

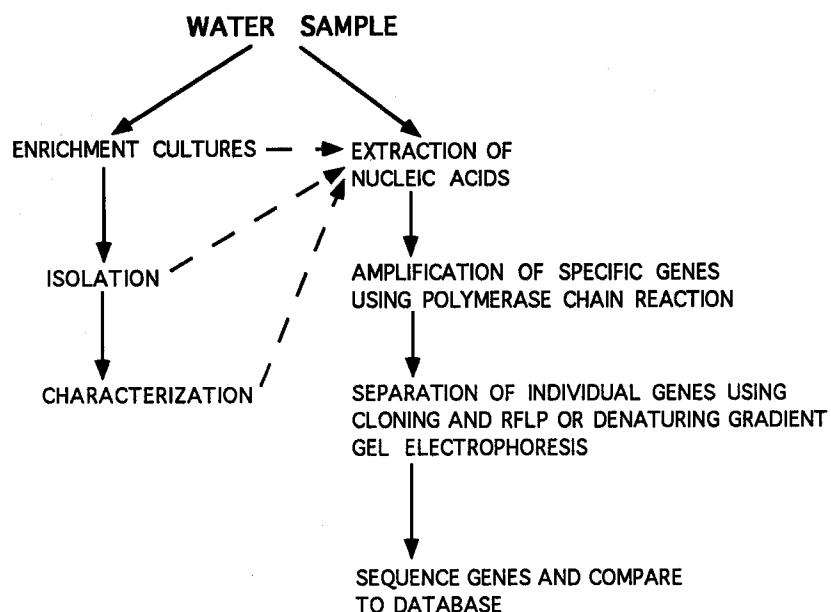


Figure 3. Flow chart showing combination of enrichment culture and molecular techniques used to examine hydrothermal vent and water column samples from Yellowstone Lake.

netically is the one that codes for a portion of the ribosome, a cellular structure where protein synthesis occurs that is found in all living organisms. In order to better study one gene, it is amplified using a process called the polymerase chain reaction (PCR). For a complete description of the process see the article by Mullis (1990). To amplify a certain gene, small pieces of DNA, called *primers*, are used. The primers are designed to be specific for the gene in question and are complementary to short sequences of the gene. They initiate making a copy of the gene of interest, which in the PCR is repeated many times. Amplification of the gene with the PCR results in billions of copies of the gene, making it easier to work with. After amplification, the sequence of bases that make up the gene is determined. So, if a bacterium has been isolated and we want to identify it using molecular tools, we determine the sequence of bases in the gene that codes for the subunit of the ribosome, called the 16S subunit, and compare this sequence to other known sequences that exist in databases. From this comparison we can examine the relatedness of one bacterium to another, or to a whole range of other bacteria, or even resolve its identity (Amann et al. 1995).

The strength of the molecular–noncultural methodology is that bacteria do not have to be grown or isolated before they can be studied. As illustrated in Figure 3, a sample can be directly analyzed starting with the extraction of nucleic acids followed by amplification of genes, most likely the 16S ribosomal DNA (rDNA) gene, with the PCR. The situation is somewhat different from that described

above for a single bacterium. Instead of just having the gene from a single species of bacteria, when amplifying the 16S rDNA gene from the nucleic acids extracted from a natural sample, one presumably ends up with this gene from the DNA of every bacterium in the sample. This is analogous to having a large bowl of spaghetti, when what is wanted are the sequences on the individual strands of spaghetti that are each from different cells. Somehow, the strands must be separated before their sequences can be effectively analyzed.

Basically, two types of methods are used to get the single strands out of the bowl. The first is cloning. This is the insertion of the single strands into a small circle of DNA, called a *plasmid*, in a bacterium, usually a strain of *Escherichia coli*. As it grows and divides, the bacterium produces many copies of the plasmid containing the strand of DNA of interest. The gene of interest is recovered and analyzed with a treatment called *restriction fragment length polymorphism* (RFLP). This process uses enzymes called *restriction enzymes* that cut strands of DNA in very specific locations. These locations are in separate places in genes from different bacteria. Therefore, after treating the recovered cloned 16S rDNA with restriction enzymes, the patterns between clones are compared by separation in an agarose gel by a process known as *electrophoresis* (Figure 4). Because the locations where the restriction enzymes cut the DNA are in separate places in different bacteria, each different type should be represented by a distinct pattern on the gel, while those with the same pattern should represent the same bacterium. Examination of the different RFLP patterns from two vent water samples suggests that the bacterial diversity in the vents is quite distinct (Figure 5). However, this information needs to be confirmed after the 16S rDNA clones are

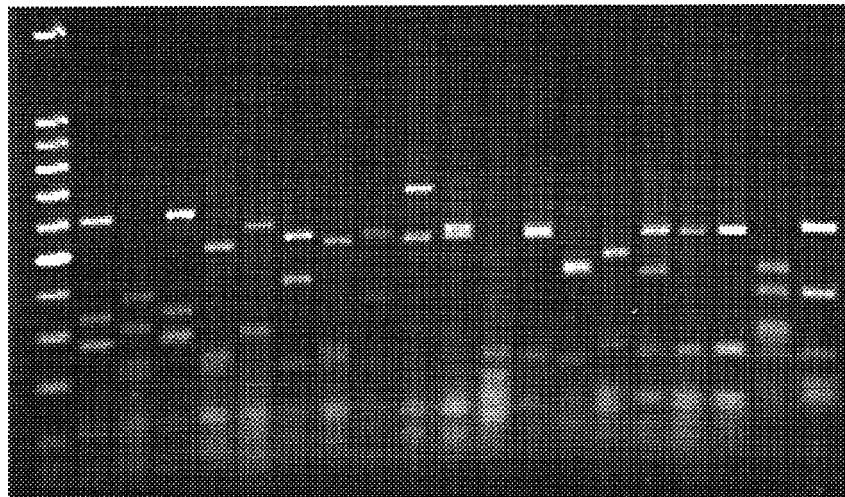


Figure 4. Example of a restriction fragment length polymorphism (RFLP) pattern from a clone library created after amplification using the polymerase chain reaction (PCR) of DNA extracted from a hydrothermal vent water sample. Of the 19 patterns generated, 15 appear to be distinct, indicating a diverse bacterial population.

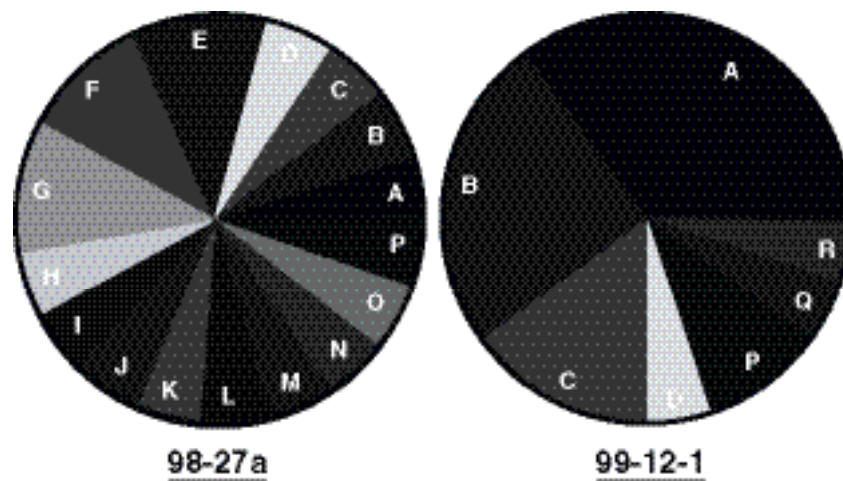


Figure 5. Comparison of RFLP patterns from two separate hydrothermal vents. The size of each pie piece indicates the proportion of the total number of clones examined with the same RFLP pattern. Clearly the diversity of bacteria in the two vents is different.

sequenced and the sequences compared. We have used, and are continuing to use, this approach to examine the diversity of *Bacteria* and *Archaea* both in hydrothermal vent waters and in the water column.

The second method involves separating the amplified DNA in gel electrophoresis. One way to do this is by what is called *denaturing gradient gel electrophoresis* (DGGE; e.g., Ferris et al. 1996). Each species of bacterium in a mixed microbial community will have a different sequence in its 16S rDNA gene. These can be separated into distinct bands in an acrylamide gel that contains an increasing gradient of a denaturant; due to their composition, each will denature and stop at a different concentration of denaturant in the gel. Each distinct band in the gel may represent a different type of bacterium. This can be confirmed by excising the bands and sequencing them. Currently, this technique is also being used on samples collected from Yellowstone Lake.

Molecular Analyses to Study Microbial Distribution

In addition to examining microbial diversity, molecular techniques can also be used to determine the presence and distribution of microorganisms with specific metabolic activities. One example is a gene for an enzyme that is involved in the oxidation of methane. The enzyme is called *methane monooxygenase* and is found in the bacteria that utilize methane as a source of both energy and carbon. These bacteria are called *methanotrophs* and may be important in parts of Yellowstone Lake because of the presence of methane in both water column and hydrothermal vent samples from some of the lake basins (Remsen et al. 1990). By taking the DNA extracted from a water sample (Figure 3) the genes for the methane monooxygenase can be amplified using specific primers (Cheng et al. 1999). By serially diluting the DNA before the PCR amplification, the number

of copies of the gene in a sample can be determined by most probable number (MPN) PCR based on the analysis of replicates diluted to extinction (e.g., Fode-Vaughan et al. 2001). In other words, the dilutions in which a signal is detected after amplification are representative of the concentration of the gene in the sample. An example using the primers for the methane monooxygenase on a water sample from Yellowstone Lake is presented in Figure 6. This methodology will allow the comparison of the distribution of the gene copies with the concentration of methane in water samples.

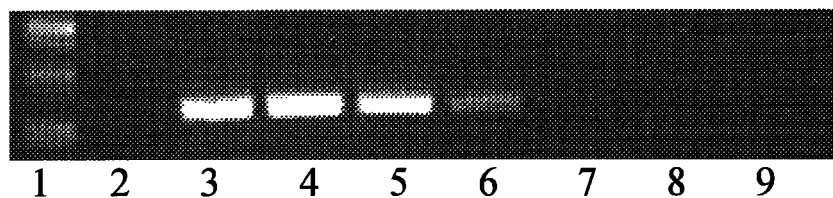


Figure 6. Example of a serial dilution of DNA extracted from a Yellowstone Lake water sample followed by amplification using the PCR of genes specific for the particulate methane monooxygenase enzyme, which is found in the vast majority of bacteria that utilize methane for both a source of energy and carbon. The last dilution (Lane 7, 1:10,000 dilution) in which a signal is amplified is representative of the concentration of the gene in the extracted DNA. Lane 1, DNA size markers; Lane 2, no DNA control; Lane 3, undiluted DNA from sample; Lane 4, 1:10 dilution; Lane 5, 1:100 dilution; Lane 6, 1:1000 dilution; Lane 7, 1:10,000 dilution; Lane 8, 1:100,000 dilution; Lane 9, 1:1,000,000 dilution.

A New Genus from Yellowstone Lake: *Thermodesulfovibrio*

Are there new microorganisms in Yellowstone Lake? In this case, the word “new” merely implies that they have not been previously isolated and characterized by humans. Any “new” microorganisms have probably been around for a very long time. The terrestrial thermal features of Yellowstone National Park have long been the source of a variety of novel microorganisms (e.g., Brock 1994). This should also be true for the hydrothermal features of Yellowstone Lake. An example of a new microorganism isolated from a hydrothermal vent in Sedge Bay is the obligate anaerobic thermophilic bacterium *Thermodesulfovibrio yellowstonii* (Henry et al. 1994; Maki 2001). This bacterium (Figure 7) has an optimum growth temperature of 65°C, reduces sulfate to sulfide, and oxidizes some organic carbon sources (Henry et al. 1994; Maki 2001). Analysis of its 16S rDNA sequence reveals it to be a member of the phylum *Nitrospirae*, a deeply branching group of the *Bacteria* domain (Maki 2001). Since its isolation and characterization (Henry et al. 1994), the 16S rDNA sequence for the genus *Thermodesulfovibrio* has been reported from a terrestrial hot spring in Yellowstone National Park (Hugenholtz et al. 1998) and thermophilic granular sludges (Sekiguchi et al. 1998). In addition, a second species, *Thermodesulfovibrio islandicus*, has been isolated from a microbial mat in a thermal spring in Iceland (Sonne-Hansen and Ahring 1999). It's clear that this bac-

terium, originally isolated from Yellowstone Lake, represents a new genus that has a worldwide distribution.

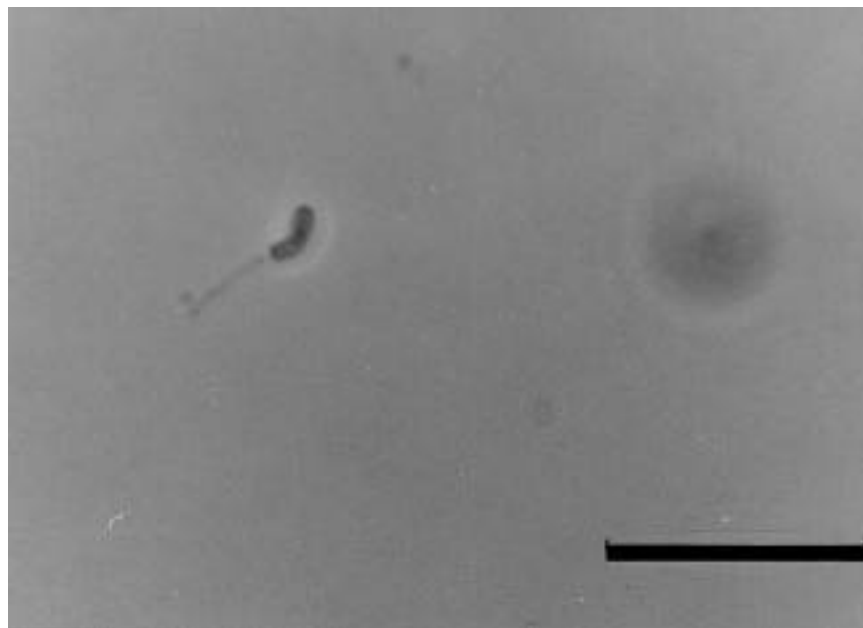


Figure 7. Photomicrograph of *Thermodesulfovibrio yellowstonii* taken with a phase contrast microscope after using a flagella stain. Bar = 10 μ m.

Conclusions

For a microbial ecologist, Yellowstone Lake represents both a challenge and an opportunity. The challenge comes in effectively collecting samples from some of the difficult locations the vents are found in. The opportunity is in the potential of finding some unusual new microorganisms. The chemical variety of geothermal features on the bottom of the lake suggest that they will be as important to microbial ecology, and microbiology in general, as the terrestrial hot springs, geysers, fumaroles, and mudpots in the rest of Yellowstone National Park have been. The molecular approaches we have taken, although many of the studies are still preliminary in nature, have indicated a wide diversity of both *Archaea* and *Bacteria* associated with the vents. Although getting all of these bacteria into pure culture is highly unlikely, through enrichment cultures and isolations there is a strong possibility in finding some bacteria that have not been previously described. The lake and its hydrothermal features should be a source of fascinating results for some time to come.

Acknowledgments

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An Archeological Investigation of a Historic Refuse Dump Associated with the Yellowstone Lake Hotel

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Abstract

In the fall of 2000, while installing a grease trap behind the Yellowstone Lake Hotel, contractors uncovered a historic trash dump overflowing with artifacts, now known as archeological site 48YE825. Cultural resources staff came to the site and collected diagnostic artifacts, such as those with distinct maker's marks, that would be useful in dating the trash pit. These artifacts included glass bottles, china, bricks, and metal objects. During early 2001, the artifacts were cleaned and analyzed in the Yellowstone National Park archeological laboratory. As analysis progressed, it became obvious that the assemblage was indeed associated with the Yellowstone Lake Hotel. It appears that the site dates to the early 20th century, approximately 1915 to 1920. This paper will present some of the more interesting information revealed by artifact analysis, together with some little-known facts about the early years of the hotel.

Historical Background

The Yellowstone Lake Hotel is the oldest standing hotel in the park, originally built between 1889 and 1891. It has undergone numerous renovations, additions, and subtractions over the years. The first addition was made in 1895, and the first major renovation occurred in 1904–1905 under the direction of Robert Reamer, the renowned park architect. Over the years, he did numerous other renovations on the building. The current hotel looks nothing like the original building, which was quite plain. Much of the following information was abstracted from the Yellowstone Lake Hotel National Register of Historic Places eligibility study, on file at the park.

When Yellowstone National Park was established in 1872, there was only one small hotel in the area, the McCartney Hotel, which was located near Mammoth Hot Springs. Shortly after, two individuals were given leases to build hotels, one along the road to Cooke City, and two along the Firehole River. In 1883, the Northern Pacific Railroad built a line to the northern boundary of the park, just west of current-day Gardiner, Montana. Now that they had access to the park, they wanted visitors to travel their lines and experience “Wonderland,” as the railroad called Yellowstone. The interests of the railroad led to much of the building that occurred within the park in later years.

In the same year that the railroad to the northern boundary was finished, the Department of the Interior leased several plots of land to the Yellowstone National Park Improvement Company, with the intent of having them build hotels for visitors. Money problems held up construction, and by 1886 only one

hotel, that at Mammoth Hot Springs, had been started. The Yellowstone Park Association (YPA), run by Charles Gibson, took over the leases and worked with the Northern Pacific Railroad Company to get money to build the hotels. In 1889, work on the Yellowstone Lake Hotel was begun.

The Yellowstone Lake Hotel was built over the course of two years. Although original blueprints for the hotel were not uncovered during this study, drawings of the floor plans were found. There were numerous complaints about the work being done; one writer claimed that he could kick the foundation out from under the building. There were other problems with shipments of supplies not coming in, or being incomplete, and workers who were drunkards (Dittl and Mallmann 1987). Two similar hotels were being built in the park at the same time: the Canyon Hotel, which opened in 1890, and the Fountain Hotel, which opened in the same year as the Lake Hotel. These buildings all had a similar design, and one foreman was in charge of all of the construction. However, the early version of the Yellowstone Lake Hotel was nothing like the Neocolonial monolith that Reamer eventually molded from it. Someone once described the original, simple building as “a Plain Jane three-story shoebox, with windows” (Mohr 1998).

Once open for business, visitors immediately started coming to the Lake Hotel. The hotels in the park were built to be about a day’s ride from one another, and business was brisk. Various minor renovations were made, and in 1904-1905, Reamer, who had just finished the Old Faithful Inn, started working on the Yellowstone Lake Hotel. He transformed this typical railroad rest stop into a stylish respite in the park’s interior. As with his other buildings, Reamer came back numerous times over the century to renovate and remodel the Lake Hotel. During his first attempt, he extended the roofline in three areas, with Ionic columns supporting it, added false balconies to some of the windows, and decorative moldings elsewhere. A wing was also added to the building at this time, as the hotel was far too small to house all of the people interested in visiting the park. While this was occurring, the original fireplaces were also taken out, as evidenced by floor plans and photographs. During a later renovation, Reamer put in another fireplace in a slightly different location, which is there to this day. Over time, the hotel has become more elaborate and is by far the most elegant hotel in the park today.

Mitigation of Archeological Site 48YE825

Yellowstone Lake Hotel and several nearby buildings have been listed on the National Register of Historic Places as a historic district. The site number for the historic district is 48YE825, and the trash dump is considered an archeological component of the district. The archeological site was uncovered during the installation of a grease trap behind the hotel. Maintenance staff noticed artifacts in the soil and stopped excavating. Ann Johnson and Lon Johnson, cultural resources staffers for the park, came to the site and collected what artifacts they could. As much of the soil had been pulled out by a backhoe, there was no context for the artifacts, and no stratigraphy was visible at the time of artifact retrieval. The majority of china was found piled together in one section of the site, but the other

materials, such as glass bottles, appeared to be scattered about. Due to the lack of context and limited time, artifacts with distinct maker's marks or datable properties were the focus of collections at the site. Based on the diagnostic artifacts, it appears that the site was used for only a short time, perhaps a single dumping episode, except for two outlying artifacts, which will be discussed later.

Based on the soil consistency and odor, Ann Johnson believes the site to have been a cesspool at some point. For this reason, all artifacts were soaked in bleach water, and gloves and masks were worn throughout the artifact cleaning process. Artifacts were then labeled and catalogued, and are now part of the Yellowstone National Park museum collection.

Artifact Analysis

Over the course of several months, all of the artifacts collected from 48YE825 were analyzed in the Yellowstone National Park archeological laboratory. One of the first questions posed was the origin of the artifacts. Although they were found behind the Yellowstone Lake Hotel, evidence was necessary to determine that the artifacts were in fact associated with the hotel. The first identifiable artifact associated with the hotel was a metal key chain from Room 249 of the hotel itself. Although there is no key attached to it, the artifact was compared with a non-archeological key chain in the park's museum, which dates to the early 1920s. Both are the same shape and style, with slight changes in text presentation. Both items say "Yellowstone Lake Hotel" and "Y.P.A." (Yellowstone Park Association), although the archeological specimen has excessive punctuation ("Yellowstone, Lake. Hotel"), suggesting it is from a slightly earlier period (Susan Kraft, personal communication 2001).

Other artifacts confirmed the pit as being associated with the hotel. The majority of china (22 pieces) found in the midden had the maker's mark of the Greenwood China Company, Trenton, New Jersey. This company specialized in mass-produced hotel wares. The United States Army also used Greenwood china while it resided in the park until 1916, but it appears that the army added an additional mark to its china, such as "Quartermaster's Corps." It is interesting to note that almost all of the pieces of china from the site are virtually whole, with only a few chips on each one.

Other items found among the refuse included pieces of building materials, including some burned wood, a ceramic insulator, two firebricks, and a pressed tile. It was the two bricks and the tile that led to an unnecessary and overextensive study of the early period of the Yellowstone Lake Hotel. Firebrick, as the name implies, is generally used for fireplaces and chimneys. The two firebricks found at 48YE825 were made by the Evens and Howard Company of St. Louis. Many people know of the beautiful fireplace that Robert Reamer added to the Yellowstone Lake Hotel in 1923. It was first thought that the bricks were leftovers from this fireplace, but all of the other diagnostic artifacts suggest a pre-1920 date for the refuse pile. There are no other fireplaces in the hotel, so where did the firebricks come from? The Montana Historical Society's copies of the original floor plans showed that the original building had two chimneys. The first

was associated with the bakeshop; the second was for three fireplaces, one in the first-floor lobby, and two on the second floor, in the parlor and the writing room. In 1904–1905, when Reamer renovated the hotel, he removed the fireplaces, along with the chimneys, as determined by floor plans and photographs. It is probable that the bricks found in the trash pit were from either the bakeshop chimney or one of these early fireplaces. In April 2001, Lon Johnson, the park's historical architect, and I searched the attic of the Lake Hotel looking for possible remnants of the chimneys, but to no avail. We also looked at Reamer's fireplace, and there were no maker's marks visible on the bricks. This is not the case for his fireplace at Old Faithful Inn, ca. 1903, where "Evens & Howard of St. Louis" is visible on every brick within the fireplace (yes, the beautiful stone fireplace at Old Faithful Inn is, in fact, lined with brick). At this point we can surmise that the firebricks found at 48YE825 are likely remnants of one of the original chimneys from the Lake Hotel, unless they are from a later, as of yet unknown fireplace.

The tile found at 48YE825 is also of interest, and also suggests probable evidence for an earlier fireplace. The tile is rectangular and has a plain, very dark green, almost black, appearance, and was made by the American Encaustic Tile Company, of Zanesville, Ohio. Photographs and a description of the tile were sent to several art tile collectors, who concluded that it appears to be the type used as fireplace border tile (Richard Mohr, personal communication 2001). Although tiles could also have been used for decoration in other areas, especially bathrooms, this particular type of tile is likely from a fireplace border. Reamer's fireplace has no tiles like this in association with it. Although the tile could not be dated to a particular year, the range for this tile does go back far enough that the tile could be from the first construction of the hotel. Could this tile then be from one of the three original fireplaces in the hotel? Unfortunately, no photographs or sketches of the original fireplaces have yet been found that can confirm or dismiss this possibility.

As interesting as all of this may be, as an anthropologist, building materials and architecture are not the main focus of my research. The real question I am interested in answering is, "What do the artifacts found tell us about the people who were here?" This question can be answered in part by a discussion of some of the other artifacts. Rather than sort them out by material, I will discuss various themes of use. The material from which an object was made is not as important as what it was used for. We must be cautious, however, in suggesting use, especially with the glass bottles. Until Prohibition ended, glass bottles were often reused and filled with materials other than those they were originally intended for. When discussing bottles, if there is no residue, I will only be talking about the original use of the bottle. It may or may not have been used for this purpose just before it was thrown out.

One of the most interesting themes is that of personal care, meaning hygiene, health, and cosmetic materials. A large quantity of material relating to these topics was found, including a soap dish, four Listerine bottles, several cologne and perfume bottles, a Vaseline jar, bottles for Bromo Caffeine and Bromo Seltzer,

and several facial cream containers, including Richard Hudnut's "Marvelous Cold Cream." Numerous other bottles and containers appear to have been medicine or cosmetic containers, but they are not embossed, and no labels remain to identify their former contents. Both the Vaseline container and one of the Listerine bottles, which was corked, still held their original contents. A reliable date of post-1908 was put on the Vaseline jar, as it had a screw-cap finish, which was not used by its manufacturer until that year (Fike 1987, 186). With the large quantity of cosmetic materials, it is curious to wonder if guests brought all of these items in, or whether staff of the hotel used them. These could be remnants from the women's living quarters that were once in the attic of the hotel. Regardless, it seems that people in the interior of the park, whether visiting or residing there, were very concerned about their appearance and physical well-being.

Two other areas of interest that led to unusual artifact identifications were transportation and recreation. An engine crank was discovered, which may or may not be from a vehicle, along with several other items, which appear to be battery and hood parts. Automobiles were not allowed into Yellowstone National Park until 1915, and the other items, in conjunction with the engine crank, suggest that at least some of them are indeed from a vehicle. Two horseshoes were also found in the trash. Two recreational items of note are fishing rod ferrules. One is of an older style pole that had a solid wood shaft, while the other ferrule was from a pole that had six pieces of bamboo held together with a pin, which is the type of pole still used today. Both still had woody material in them.

The final theme I would like to look at is food and drink. By far, the majority of artifacts were beverage bottles. Several pieces of Greenwood china were found as well, most of them stacked together. These pieces ranged in size from small sauce dishes to dinner platters. Most pieces were whole, though they had a few chips. It is interesting to note that one teacup and one saucer both had burned material in them. Some china fragments not made by Greenwood were also found, though these were much smaller, incomplete pieces.

An unusual food item was the remnants of a chocolate box. Stuffed inside one cylindrical glass container were the remains of a paper chocolate box and its decomposed wrappers. The box was from J. G. McDonald Chocolates, out of Salt Lake City, Utah. The container that held the chocolate box is some sort of condiment container. Several varieties were found at the site, including a ketchup bottle. Two sawn bones of large mammals were also among the food-related artifacts.

Beverage bottles were some of the most numerous artifacts. Several alcohol bottles were found, from large whisky bottles to flasks to plain brown beer bottles. Three of the most unusual bottles were made by EJ Burke and company. These bottles were made with an automatic bottle machine, which dates them to post-1903, and probably a bit later, as large bottles could not be made with automatic bottle machines in the earliest years. The olive green glass has large air bubbles and wrinkles on it, a problem that only occurred during the first years of production on the automatic bottle machine. EJ Burke has a very unusual mak-

ers mark on the base, in the shape of a cat. These bottles were used to bottle either Guinness or Bass Ale (Toulouse 1971).

Another unusual collection was that of grape juice bottles. For some unknown reason, 11 embossed grape juice bottles were thrown in this trash midden, the largest quantity of bottles associated with one beverage type at the site. Each bottle was a small, clear, four-ounce bottle. Again, these proved to be a reliable dating tool. Two bottles were Welch's bottles, while the other nine were for Royal Purple Grape Juice. The trademark for Royal Purple was established in 1916 (registration nos. 75190, 276279, and 392008) by the United Grape Products Sales Corporation of Buffalo, New York. However, no information on the company has been found, and the history of this beverage remains hidden at this time. The form and quality of the bottles also match a post-1916 date.

Discussion

No conclusive reason for the disposal of the artifacts at site 48YE825 has yet come to light. Included in the collection are a manure pitchfork, pharmaceutical bottles, chipped china, building materials, and a wide variety of other artifacts one would rarely group together. The best explanation developed thus far for their common disposal is that these items represent an end-of-the-season clean out of the Lake Hotel. This would account for the wide variety and large quantity of complete items in the trash midden. The variety of items does not seem to correlate well with either living quarters alone or an area such as the kitchen; there is too much variety. There are probably other plausible explanations for the variety, quantity, and quality of artifacts in the midden, but this seems the most probable.

The two outlying artifacts found in the collection are a Mission Beverages bottle and the base of a vase or flowerpot with the mark of the Yellowstone Park Company. The Mission Beverages Company was not formed until the late 1920s, and the Yellowstone Park Company was not established until 1936. However, the majority of artifacts in the collection strongly suggest an earlier date for the site. After Prohibition ended, it was required that bottles be embossed with the phrase "not for reuse or resale," which is not on any of the bottles in the collection. Surely if the collection was from the late 1930s, the majority of bottles would have this mark. Many of the companies that were identified by maker's marks at this site went out of business during the Great Depression as well. Further, several of the bottles in the collection were not made on automatic bottle machines, and those that were so made showed signs of being from the earliest periods of its use. This combination of bottles suggests a date from the period 1910–1920. Also, the Royal Purple bottles and the automobile parts suggest a date after 1915. As this was a salvage excavation, artifact layers, had there been any, were mixed together by the backhoe. I believe the two anomalous artifacts to be outliers that were located above the trash midden and were mixed into the collection accidentally.

Conclusion

The Yellowstone Lake Hotel has a long and intriguing history, made more interesting by the use of archeology. Archeological site 48YE825, an early twentieth-century trash dump associated with the hotel, reveals information about part of the area's history that is often overlooked in documents: the everyday activities of visitors and staff in the park. It does not give us more information about presidential visits or unusual bear encounters; rather, the comings and goings of the average people at the Lake Hotel, what they ate, the perfumes they wore, and their passions for grape juice and gargling. Although some people chide historical archeologists about being "garbage-pickers" and "dumpster-divers," the information uncovered in archeological refuse can give new insights into the history of an area. When people throw items out, they do not expect anyone to come along 80 or 8,000 years later to look at them, so these objects are often less biased than historical documents. Thus, items in historic trash piles can tell us a little more about the people who stayed in the park, at places like the Lake Hotel. There are numerous historic sites in Yellowstone National Park; many of them are trash middens that are full of information if carefully studied as collections by archeologists. The next time you are on a backcountry trail, and you see one of these middens, don't look at it as a dirty pile of trash; think about the people who left that trash there and, unknowingly, left us a tangible piece of themselves that can be added to the historical record of Yellowstone National Park.

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Piscivorous Birds of Yellowstone Lake: Their History, Ecology, and Status

Terry McEneaney

Yellowstone Lake is truly one of the most recognizable geographic features of the Greater Yellowstone area, and, most importantly, the ecological nucleus for native fishes and piscivorous birds in Yellowstone National Park. It is home to the only current nesting colony of American white pelican (*Pelecanus erythrorhynchos*) in the National Park System. It is also unique for having the highest-elevation nesting records in North America for colonial nesting birds such as the American white pelican, double-crested cormorant (*Phalacrocorax auritis*), California gull (*Larus californicus*), common loon (*Gavia immer*), and Caspian tern (*Sterna caspia*). In excess of 50% of Yellowstone's bald eagle (*Haliaeetus leucocephalus*) and osprey (*Pandion haliaetus*) nesting pairs are currently associated with Yellowstone Lake and its piscine prey. The magnetism of this unique area for birdlife rests on its remoteness, inaccessibility, and abundant food resources. Only two native fishes are found in Yellowstone Lake: the Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) and the longnose dace (*Catostomus catostomus*). But it is the cutthroat trout biomass that is the main attraction for the piscivorous birds of Yellowstone Lake.

The piscivorous birds and the cutthroat trout of Yellowstone Lake have undergone a kaleidoscope of management practices, public attitudes, philosophical differences, exotic introductions, population changes, and distributional shifts. This paper will intertwine these points while examining the history, ecology, and status of the piscivorous avifauna of Yellowstone Lake.

History

The history, ecology, and status of the piscivorous birds of Yellowstone Lake is best understood by reviewing three important timelines: those of the park itself, of fish management in the park, and of bird management in the park.

By reviewing the Yellowstone timeline, the following events are of significance to the piscivorous nesting birds of Yellowstone Lake:

- 1872: Yellowstone National Park established;
- 1872–1935: predator control era in Yellowstone (this included pelican and eagle eradication);
- 1883: hunting in Yellowstone prohibited;
- 1916–1918: changeover in management authority from the U.S. Calvary to the National Park Service (NPS);
- 1918: Migratory Treaty Act passed, affording some protection for birdlife;
- 1941–1945: World War II;

- 1945–1972: high use of DDT in North America following World War II;
- 1953–1957: DDT spraying in the park to combat spruce budworm;
- 1988: Yellowstone wildfires; and
- 1994: first discovery of exotic lake trout, New Zealand mud snail, and whirling disease.

A review of the fish management timeline reveals the following events that have had a bearing on food abundance for the piscivorous birds of Yellowstone Lake:

- 1872–1948: no fish limits;
- 1889: U.S. Fish Commission and fish stocking program established in the park;
- 1906: 20-fish limit;
- 1948–1953: five-fish limit;
- 1953–1970: three-fish limit;
- 1970–1973: two-fish limit;
- 1973: catch-and-release fishing with size limitations; and
- 2001: catch-and-release fishing for all native fishes.

And lastly, a synopsis of the bird management timeline emphasizes important events that have affected the status of the piscivorous birds of Yellowstone Lake:

- 1890–present: pelican census conducted on the Molly Islands (Yellowstone Lake);
- 1890–1931: era of visitor disturbance on the Molly Islands;
- 1924–1931: pelican control program on the Molly Islands;
- 1945–1959: boat disturbance on and near the Molly Islands;
- 1960–present: the Molly Islands closed to the public (Figure 1);
- 1960–present: no- and slow-motor zones established on the arms of Yellowstone Lake to protect colonial nesting birds and molting waterfowl; and
- 1978–present: campsite closures on Yellowstone Lake to protect nesting ospreys, Frank Island closure to protect nesting ospreys, and Stevenson Island closure to protect nesting eagles.

Ecology

The Yellowstone cutthroat biomass on Yellowstone Lake is what attracts the richness and abundance of piscivorous birdlife. The following birds have been documented as nesting in Yellowstone and feeding on the fish of Yellowstone Lake: Caspian tern, common loon, American white pelican, California gull, double-crested cormorant, osprey, bald eagle, common merganser (*Mergus merganser*), American dipper (*Cinclus mexicanus*), great horned owl (*Bubo virginianus*), common raven (*Corvus corax*), great blue heron (*Ardea herodias*), great gray owl (*Strix nebulosa*), and belted kingfisher (*Ceryle alcyon*). However, the



Figure 1. Boat disturbance of the Molly Islands from 1945 to 1959 paved the way for a permanent half-mile closure of the islands to the public beginning in 1960.

principal piscine biomass consumers are the first seven species named. Long-term population data also exist for them, thus allowing an opportunity to review the status of each of these important piscivorous bird species. Due to space limitations, the following discussion will be limited to these seven species.

Interestingly enough, the combination of high elevation and harsh weather conditions make the Yellowstone plateau and Yellowstone Lake some of the most inhospitable places found in the temperate zone of North America for nesting birds. Yellowstone Lake typically freezes from December or January through May, thus forcing all seven species to migrate, with the exception of the bald eagle. Some pairs of bald eagles reside on the Yellowstone plateau throughout the winter, seeking out thermal and open areas with an abundance of waterfowl, fish, and carrion. Other pairs move to lower elevations of the Greater Yellowstone area, and carve out an existence there until additional areas open up on the plateau.

Fish biomass availability is critical for piscivorous birds, but the role weather plays in bird production in Yellowstone National Park cannot be overlooked. Flooding, drought, wind, snow load, rain, hail, lightning, and wildfires all play a role in the overall success or failure of each of these piscivorous bird species. These factors coupled with natural predation and human disturbance can influence the success or failure of a species in any given year.

How can these piscivorous birds feed on the same food biomass and in the

same habitat without competing with one another? The answer lies in our understanding of the ecological role each piscivorous bird species plays within a community, enabling it to survive by achieving niche separation. Our first clues to understanding the ecological role of piscivorous birds lie in the knowledge of the bathymetry of Yellowstone Lake (Figure 2). The ecological role of these species is best explained through resource partitioning. In other words, these species carve out a different part of the resource which allows them to survive.

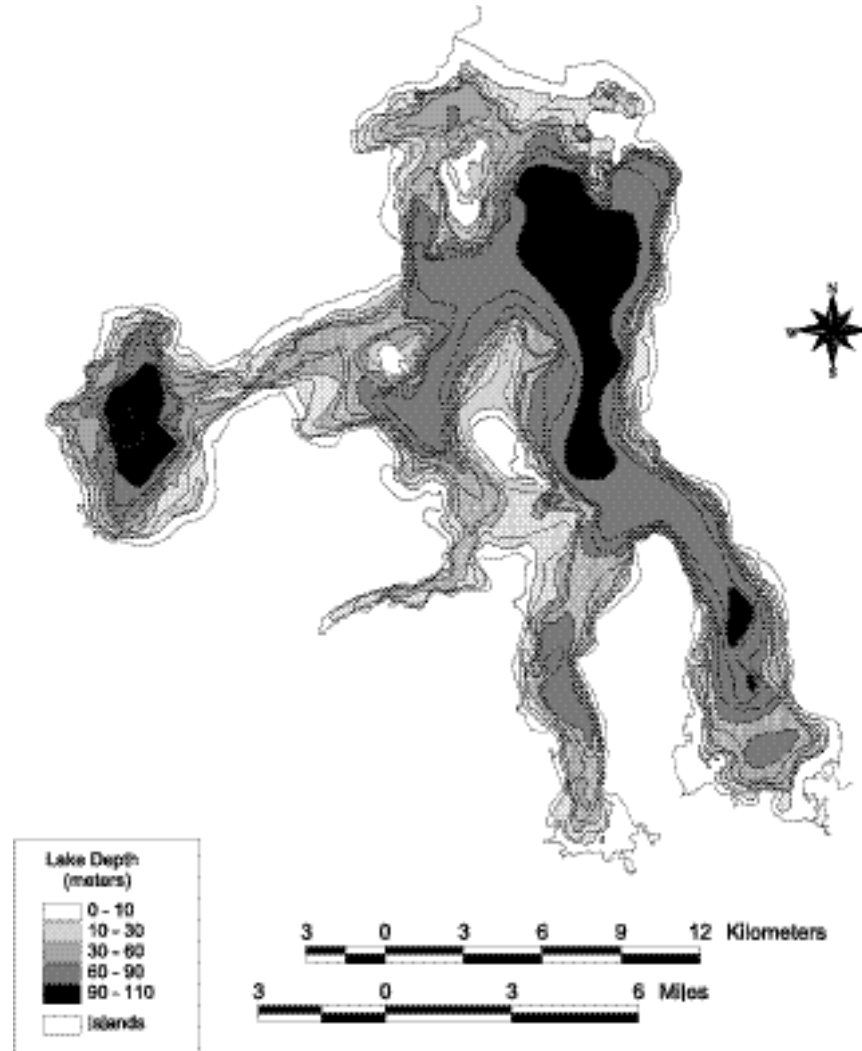


Figure 2. Bathymetry of Yellowstone Lake.

By examining resource partitioning of different lake depths by birds, we find certain birds forage or feed at different depths; thus the term *bathylacustrine foraging*. Species that are surface feeders include the California gull, American

Piscivorous Birds

Table 1. Resource partitioning through bathylacustrine foraging.

	Water depth, ft						
	Surface	0-2	2-4	4-6	6-20	20-60	60+
Common loon					•	•	•
Double-crested cormorant					•	•	•
California gull	•	•					
Caspian tern		•	•				
American white pelican	•	•	•				
Bald eagle	•	•	•				
Osprey			•	•			

white pelican, and bald eagle (Table 1). The above species also forage at depths of 0–2 ft, as does the Caspian tern. At depths of 2–4 ft, the Caspian tern, American white pelican, bald eagle, and osprey are often found foraging. Ospreys can dive deeper than bald eagles, and have been observed diving 4–6 ft into the water to secure piscine prey. Ospreys also have the ability to hover, allowing them to forage out in open waters such as are found over much of Yellowstone Lake. The deeper-water feeders are the common loon and the double-crested cormorant, foraging at levels ranging from 6 to over 60 ft deep.

Piscivorous birds have other means of resource partitioning, such as foraging for different-sized fish or allopiscine prey. Some are either specialized or generalized feeders of different-sized fish, depending on their morphology (Table 2). Common loons and double-crested cormorants usually feed on fish that are 2–9 inches in length, more commonly taking those around 6 inches in size. California

Table 2. Resource partitioning of allopiscine prey.

	Length of fish, inches				
	0-2	2-6	6-9	9-11	11+
Common loon		•	•		
Double-crested cormorant		•	•		
California gull	•	•	•	•	•
Caspian tern	•	•			
American white pelican	•	•	•	•	•
Bald eagle				•	•
Osprey			•	•	

gulls, on the other hand, are generalist feeders, consuming fish from 1 to 11+ inches in size, and can secure prey through either foraging or scavenging. Caspian terns take fish that are smaller, rarely if ever exceeding 6 inches in length. American white pelicans are opportunistic feeders and will take any size prey ranging from 1 to 11+ inches. Although they are often observed taking larger fish, smaller fish are also a part of their diet. Bald eagles typically take adult fish often exceeding 11 inches in size, and on occasion take fish as small as 9 inches. Osprey, on the other hand, take smaller, immature fish ranging from 8 to 11 inches in length.

The piscivorous birds of Yellowstone Lake also partition the resource through a variety of foraging habits or techniques (Figure 3). Bald eagles, for instance, typically hunt from an elevated perch, but also hunt in flight. Capturing fish requires diving into the water talons-first, using the wings as floats. If a fish is caught, eagles either take off with the fish in their talons or, if the fish is heavy, paddle to shore with the prey. American white pelicans stalk fish from the surface of the water. Most often they work in synchronous foraging groups, or flotillas, forcing fish to the shore by flaring their colorful feet and dipping their heads in water until they finally catch fish in their distensible pouch. Caspian terns hunt exclusively from the air, searching shorelines and shallow water areas for small schools of fish. When small fish are sighted, the terns plunge into the water before returning to normal flight with fish draped between their mandibles.

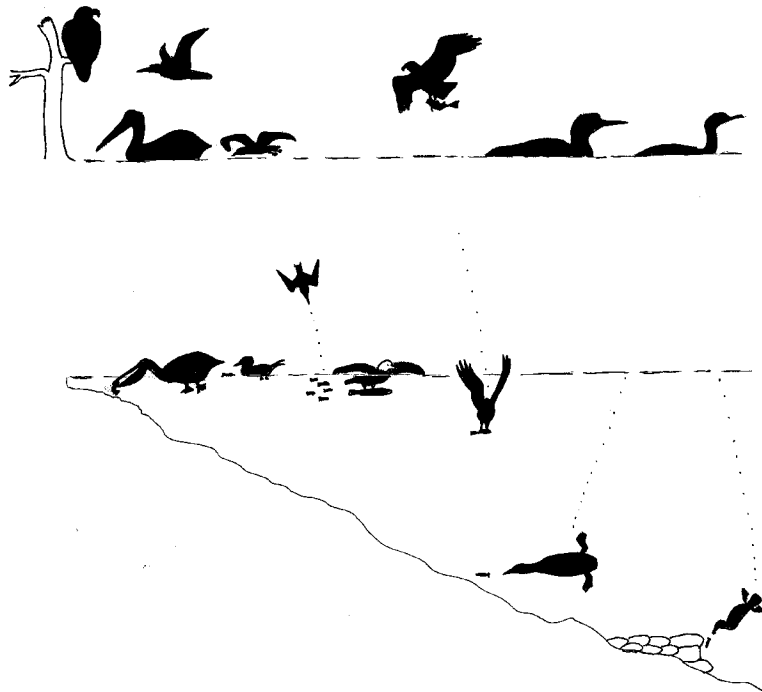


Figure 3. Resource partitioning—foraging habits.

Ospreys can hunt from an elevated perch, but most typically hunt by hovering. Once a fish is sighted, they “stair-step,” dropping in elevation until they finally plunge talons-first into the water. Osprey become totally submerged, then bob back up to the surface and use their wings to lift off. Once the fish is oriented head-first and secured, the osprey does a body shake to eliminate excess water. Common loons dive from a floating position on the surface of the water. They stalk their prey long-distance and catch up with the fish easily due to their speed. When a fish is caught, loons return to the surface where they swallow the fish whole, head-first. Double-crested cormorants also dive from a floating position on the surface of the water. They are best suited for searching the deeper, darker depths or rocky shoal areas, scouring nooks and crannies for prey at close distances. Once a fish is caught, cormorants return to the surface of the water where they, like loons, swallow their prey whole, head-first.

Lastly, resource partitioning of the nesting substrate is another way the piscivorous birds of Yellowstone Lake can exist in the same habitat (Figure 4). Bald eagles select large trees and build large platform nests down in the tree where the nest and young are shaded by the adults early in life and by branches later on. Ospreys typically build in the tops of trees or on rock pinnacles. Their nests have a telescoping profile, i.e., are smaller at the top than at the base. They normally shade the eggs and the young with their wings. Common loons nest on the water’s edge of lakes. Their nest is a simple floating mass of vegetation camouflaged and concealed by the shoreline. Caspian terns, California gulls, American white pelicans, and double-crested cormorants are colonial nesting birds, and all

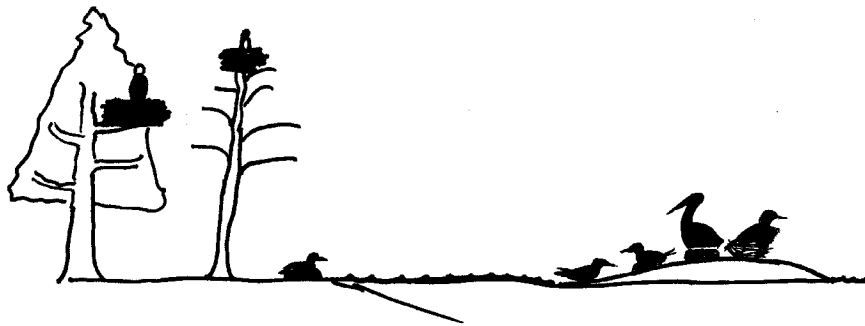


Figure 4. Resource partitioning—nesting substrate.

nest on the Molly Islands. Caspian tern nests are simple scrapes or depressions on a sandy substrate, usually on the lower points of the islands, but are heavily defended by the adults from avian predators. California gulls build very simple nests in rocky substrates midway up on the islands. American white pelicans build simple elevated mounds of sand debris and guano; they nest on the higher parts of the islands. Double-crested cormorants nest on the highest part of the islands. Their nest consists of elevated sticks and weeds cemented by guano.

Status

Determining the true status of birds requires an understanding of the many variables, both natural and anthropogenic, that influence population dynamics. A review of historical management actions, coupled with knowledge of the ecology of the bird, is of paramount importance since it fills in informational gaps regarding a particular species and creates a more complete picture of its status, both past and present.

Osprey. The osprey of Yellowstone National Park and Yellowstone Lake are doing remarkably well (Figure 5). Nesting pairs increased following the 1988 Yellowstone wildfires. Since food is highly abundant, the limiting factor continues to be availability of nest sites. Following the wildfires, snags increased and consequently so did the number of nesting pairs, since osprey most often select burned or dead trees for their nests. Heavy winds knocked down a large number of standing snags, and therefore contributed to the trough experienced in 1995 and 1996. DDT is no longer a threat as it was midway through the last century. Osprey productivity is dynamic and remains weather dependent. In 2001, there were 59 nesting pairs of osprey on Yellowstone Lake, fledging a total of 26 young.

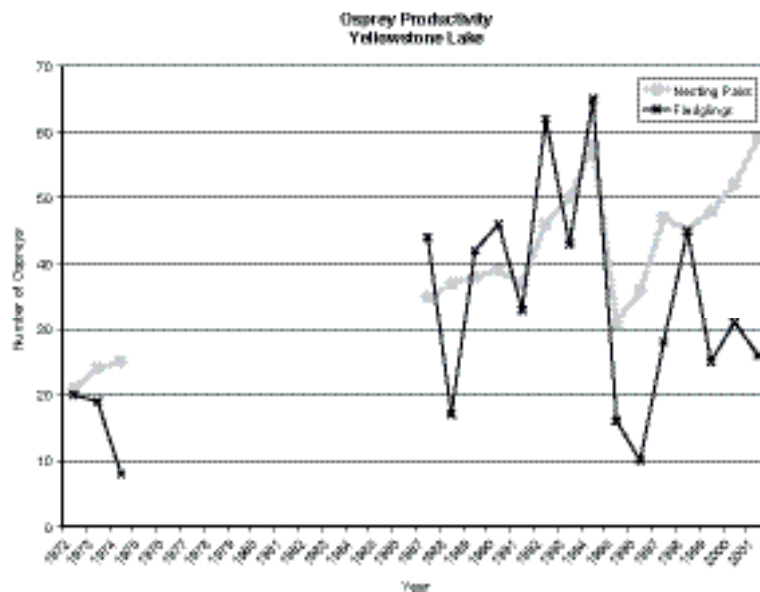


Figure 5. Osprey productivity, Yellowstone Lake, 1972–2001.

Bald eagle. Bald Eagle nesting pairs continue to gradually increase on Yellowstone Lake and throughout the park (Figure 6). Fledgling numbers rarely if ever exceed one per nest. The elimination of DDT in 1972 paved the way for the increase in numbers we experience today. Large nesting trees continue to fall down, contributing to the annual fluctuation of nesting pairs. Bald eagle produc-

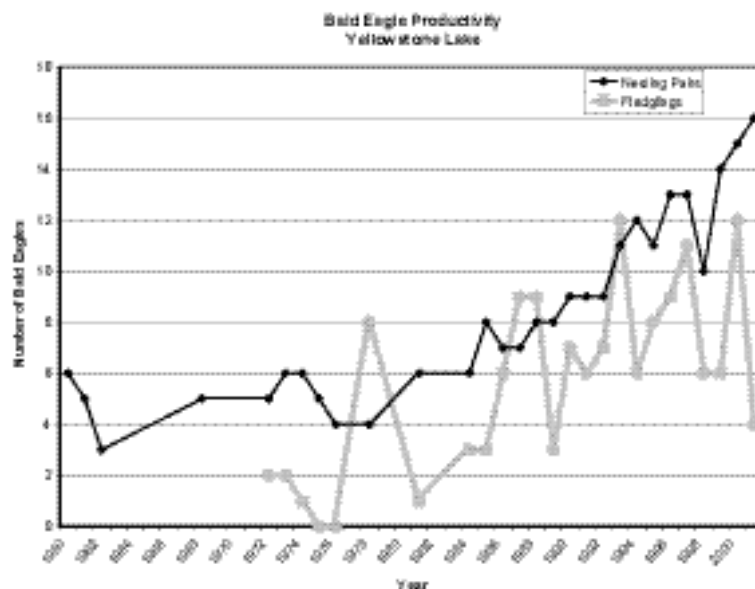


Figure 6. Bald eagle productivity, Yellowstone Lake, 1960–2001.

tivity is dynamic and highly influenced by weather. In 2001, 16 nesting pairs fledged only four eaglets.

Common loon. Only one to two common loon pairs nest on Yellowstone Lake in any given year (Figure 7). Their numbers remain relatively stable with minor fluctuations from year to year. Flooding and drought can have similar negative effects when it comes to nesting. Fledgling loons vary from 0 to 4 in any given year. In 2001, three loonlets fledged from two nests. Yellowstone Lake loons show nearly identical trends parkwide.

Caspian tern. In recent years, Caspian tern numbers have declined (Figure 8). A total of three nesting pairs fledged three young in 2001. In 1990, there were 28 nesting pairs fledging 28 young. Causes for the decline appear to be twofold: weather, in the form of flooding; and disturbance of the islands. Caspian terns are extremely sensitive to disturbance, whether it be from predators or humans. One visit to the islands during incubation or early hatching can result in failure. Even though the Molly Islands are technically closed to the public, occasionally boaters are caught on or close to the islands in a closed area. A concerted effort needs to be made to better educate the boaters of Yellowstone Lake as to the sensitivity of the Molly Islands and to better enforce the closure.

California gull. California gull numbers moderately fluctuate from year to year (Figure 9). During the 1940s, their numbers were significantly higher, which corresponded with the period of boat disturbances on the Molly Islands, allowing a feasting on eggs by predators such as gulls. In 2001, a total of 90 California gulls nested, which resulted in 95 fledglings. Since California gulls nest on the

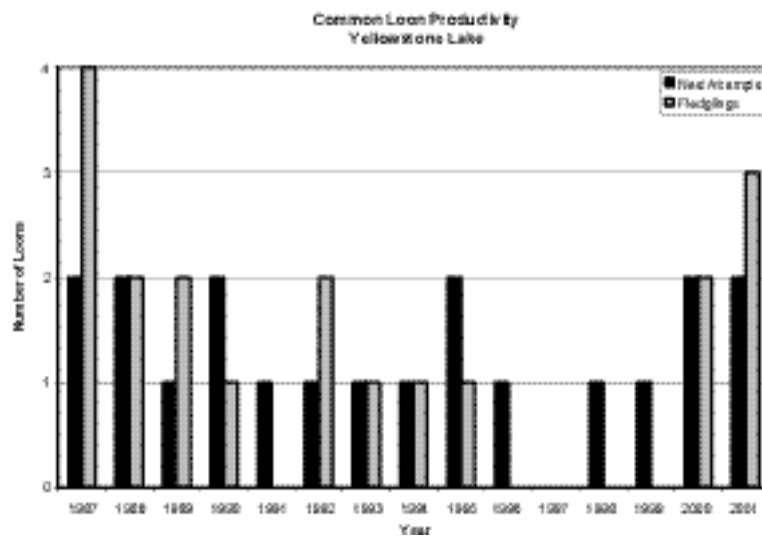


Figure 7. Common loon productivity, Yellowstone Lake, 1987–2001.

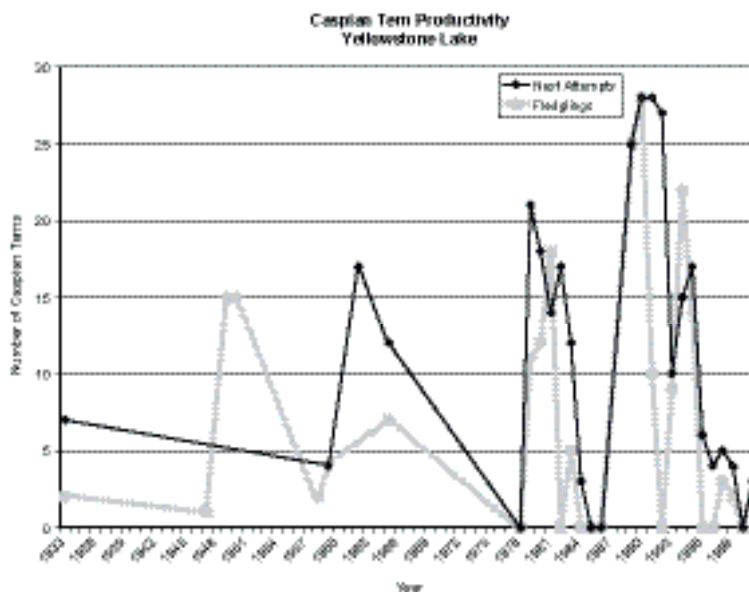


Figure 8. Caspian tern productivity, Yellowstone Lake, 1933–2001.

lower topography of the Molly Islands, they are subject to water-level fluctuations on Yellowstone Lake.

Double-crested cormorant. The double-crested cormorant has increased in Yellowstone National Park since the era of nest disturbance and DDT use ended

Piscivorous Birds

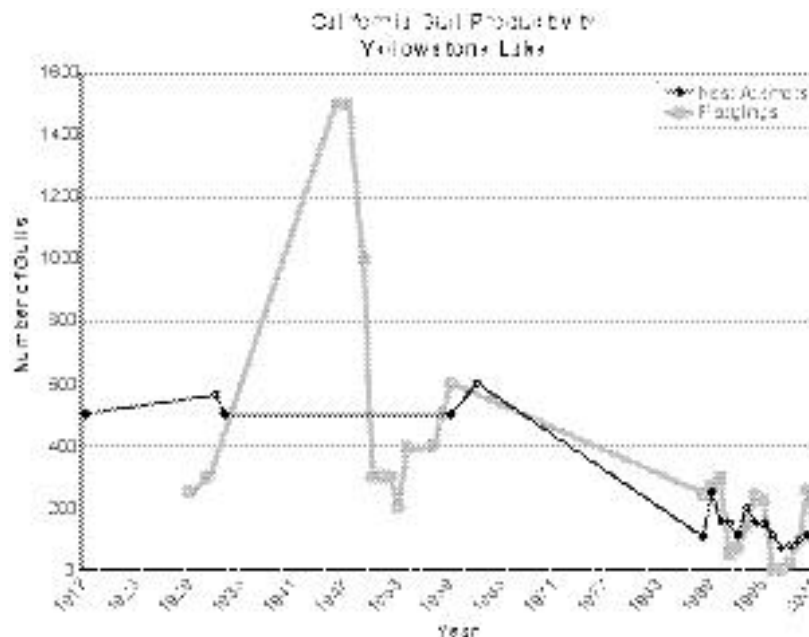


Figure 9. California gull productivity, Yellowstone Lake, 1917–2001.



Figure 10. Double-crested cormorant productivity, Yellowstone Lake, 1946–2001.

(Figure 10). Today, the number of nesting pairs and fledglings fluctuates from year to year. Flooding and disturbance are the two principal factors affecting production. In 2001, a total of 111 double-crested cormorant nests were constructed, fledging 75 young.

American white pelican. Of the piscivorous birds found on Yellowstone lake, none have a more pronounced annual fluctuation than the American White Pelican (Figure 11). Pelican control in the 1920s, followed by human disturbances in the 1940s and 1950s, kept the population at low levels. Since that time, pelican numbers have fluctuated greatly from year to year, both in the number of nesting attempts and fledged juveniles. Flooding takes its toll on pelican production, as does disturbance from either humans or predators. Pelican nest attempts

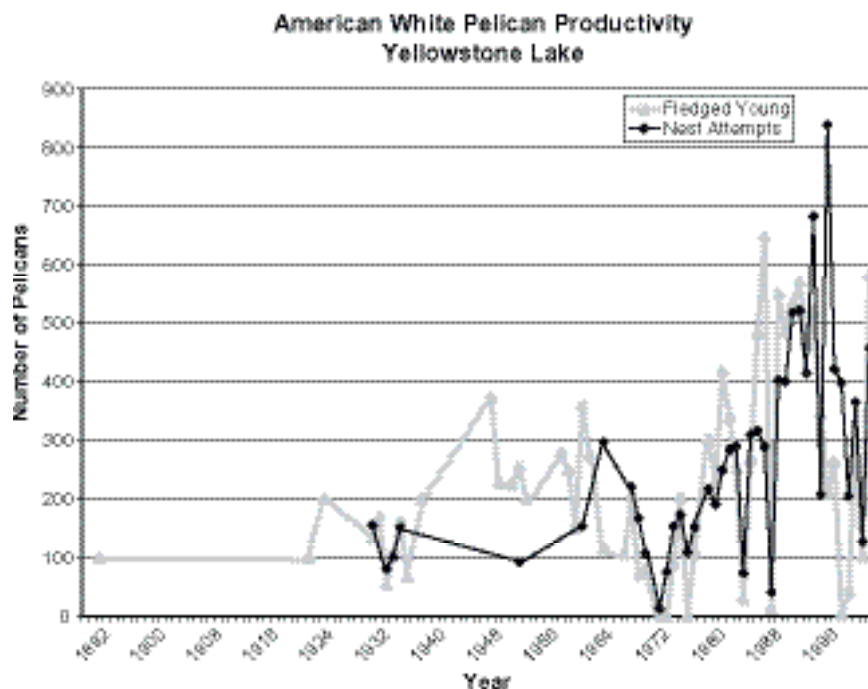


Figure 11. American white pelican productivity, Yellowstone Lake, 1892–2001.

reached their peak in 1994, when 839 pairs nested, whereas peak production occurred in 1985, with 650 fledged juveniles. In 2001, a total of 264 pelicans nested, fledging 205 young.

Yellowstone Lake is a unique, natural, dynamic environment. The importance of fish and fish biomass for the piscivorous birds of Yellowstone Lake cannot be overemphasized. The shallow-spawning cutthroat trout of the lake provide tremendous food biomass for birds and mammals. The discovery of lake trout in Yellowstone Lake in 1994, combined with that of the New Zealand mud snail and whirling disease in the same year, only add fuel to concerns about the ecology of

aquatic environments in Yellowstone, such as Yellowstone Lake. On the horizon are other serious threats, such as acid rain, global warming, climate change, methyl mercury contamination from geothermal deposits and natural wildfires, and increases in human visitation to the park.

Making doom-and-gloom predictions about the future of Yellowstone Lake piscivorous birds is not recommended, since there are too many variables to comprehend. Yellowstone Lake is a dynamic aquatic environment, so it is important that we let it play out as naturally as possible with little human intervention.

Summary

The piscivorous birds of Yellowstone Lake have undergone a kaleidoscope of management practices, public attitudes, philosophical differences, exotic introductions, population changes, and distributional shifts. When reviewing the history, ecology, and status of the piscivorous birds of Yellowstone Lake, we find bald eagle and osprey numbers incrementally increasing in recent years. Double-crested cormorant numbers have improved since the first half of the 20th century; however, these numbers show that their populations are starting to stabilize. On the other hand, Caspian tern numbers are decreasing, primarily due to weather and disturbance. California gull numbers have decreased from the mid-20th century, but have now reached a more natural condition. Common loon numbers fluctuate ever so slightly from year to year, whereas American white pelican numbers have improved from the first half of the 20th century. However, they fluctuate wildly from year to year. After 16 years of study, it becomes apparent that weather highly influences bird productivity in Yellowstone.

How do the piscivorous birds of Yellowstone Lake occupy the same habitat? What type of niches do they occupy? This is best explained through resource partitioning of fish prey sizes, foraging at different water depths, foraging using specialized techniques, and selecting different nest substrates, to name a few.

What about the doom-and-gloom predictions for the piscivorous birds of Yellowstone Lake? Does the presence of exotic organisms in an environment automatically mean a decline in indigenous species? Will we lose bird species richness? Probably not. What about species abundance? Perhaps, but we don't know to what degree and what time frame we are talking about. Predictions are useless without completely understanding the byzantine variables involved. The safest action one can take is to just let things play out. Only time will tell. We have no idea what other variables are on the horizon. But in the meantime, we need to keep the human variables to an absolute minimum.

Two thousand years ago, the Roman prescient Lucretius proclaimed, "Once something changes it can never be again what it was before." The same can be said for the ecological complexity of Yellowstone Lake. Monitoring and mitigating for the degree and rapidity by which Yellowstone Lake changes will be the ultimate challenge for this generation of ecologists and those yet to come.

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Recent Changes in Population Distribution: The Pelican Bison and the Domino Effect

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Abstract

Bison apparently have wintered for centuries in the Pelican Valley area of Yellowstone National Park. Compared with the other locations where bison winter in the park, Pelican Valley routinely experiences the most severe conditions. Nevertheless, a population has survived there because of the presence of geothermally influenced sites. Until 1980, these bison were isolated in winter by deep snows. Both winter and summer range use showed broadly consistent and predictable patterns, as did seasonal movements between range use areas. In the early 1980s, gradual but escalating changes in the bison population became apparent. Annual winter use of foraging areas by the Pelican bison expanded west from traditionally used, geothermally influenced places near the shore of Yellowstone Lake to sedge areas near the mouth of Pelican Creek, Lake area, and on to Hayden Valley. Because Hayden Valley (part of the Mary Mountain unit) was occupied already by wintering bison, as more shifted from Pelican Valley, more bison moved into the Firehole. They also moved earlier. The process of winter range expansion was coupled with a population increase, and more bison moved further west to Madison Junction and beyond, to spill over the park's west boundary into Montana. We term this cascading pattern of population increase *the domino effect*. Concomitantly with the winter westward shift, summer distributions also changed dramatically. The Pelican bison no longer crossed the Mirror Plateau to reach subalpine areas in the upper Lamar country in early summer. Instead, increasing numbers of bison concentrated in Hayden Valley during the breeding season. Some then moved back to the Pelican area before winter set in. With an increased bison population park-wide, numbers also spread across the Lamar Valley in midsummer, and appeared in meadows west and north of Madison Junction where summer use was not recorded previously. Over roughly 20 years, an apparent ecosystem change has occurred involving the bison of the interior of Yellowstone National Park. Although complex and interactive factors involving climatic variation and bison social behavior seem likely to have had a role, another element may have been human-generated. In recent decades, recreational use by people of the park's interior road system in winter resulted in compacted snow surfaces that, in certain locations and times, provided ready-made travel linkages between locations where bison preferred to be. This was seen first in 1980 with bison located on the packed road surface west from the Mary Bay site of the traditional Pelican winter range. The observed changes may not have reached their maximum expression, but the future for the Yellowstone bison does not appear reassuring.

Introduction

A bison (*Bison bison*) population has wintered for centuries in and adjacent to Pelican Valley at the northeast corner of Yellowstone Lake (Figure 1). Compared with the other bison wintering locales in Yellowstone National Park, this area routinely experiences the most severe conditions in terms of snow depths and length of season. However, bison apparently have utilized this winter range for at least 800 years, as suggested by bones at a dated archeological site (Cannon et al. 1997). Winters toward the latter part of the 1800s frequently were more severe (Meagher and Houston 1998) than those in recent decades (and surely were during much of the Little Ice Age, roughly 1450–1750 AD), but regardless, wintering bison survived in this locale. The presence of scattered geothermal sites appears to have been key to the ability of a bison population to survive success-

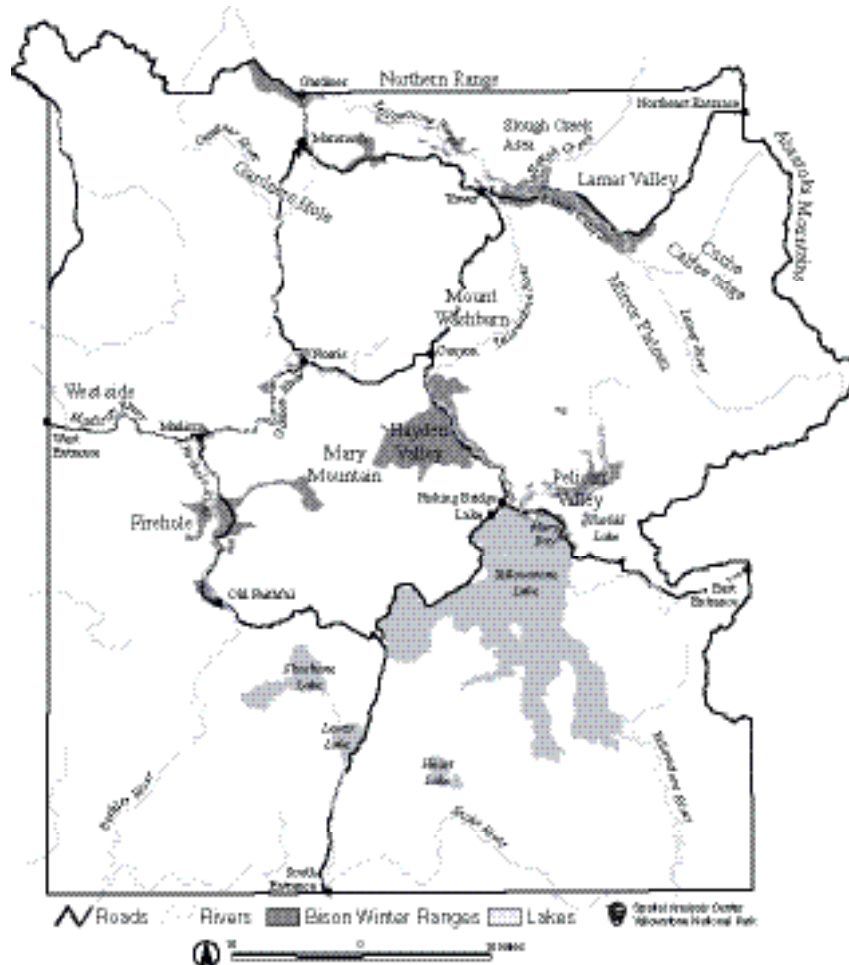


Figure 1. Key bison winter ranges and road system in Yellowstone National Park. (Yellowstone National Park GIS.)

fully through the most severe winters. (The term *geothermal sites* includes a spectrum of geothermal activity that ranges from features such as geysers to geothermally influenced foraging areas where snow depths are less, comparatively, and snow cover lasts a shorter time.) As winter progressed, mixed groups (predominantly females with juveniles and calves) commonly would forage on geothermally influenced sedge areas, and some groups would begin to fragment (stress dispersal) and scatter into small, remote geothermal sites. As conditions moderated, the bison would regroup (Meagher 1971, 1973, 1976). Since park establishment in 1872, limited historical information and subsequent administrative accounts suggest that the seasonal land-use patterns for the early park years were comparable with those described by Meagher (1973), with the Pelican bison wintering apart from other park bison, isolated by deep snows (Figure 2).

In spring (early to mid-June) the Pelican bison traditionally would leave their winter range and move in a generally northeasterly direction, sometimes traversing more than 32 km of snow and melt-water on the Mirror Plateau to cross the Lamar River, and go upward to the greening subalpine vegetation on the westward-facing lower slopes of the Absaroka Mountains. As green-up progressed, the Pelican bison would move higher, usually arriving at the east boundary of the park toward the end of July and early August (Figure 3). By this time, breeding

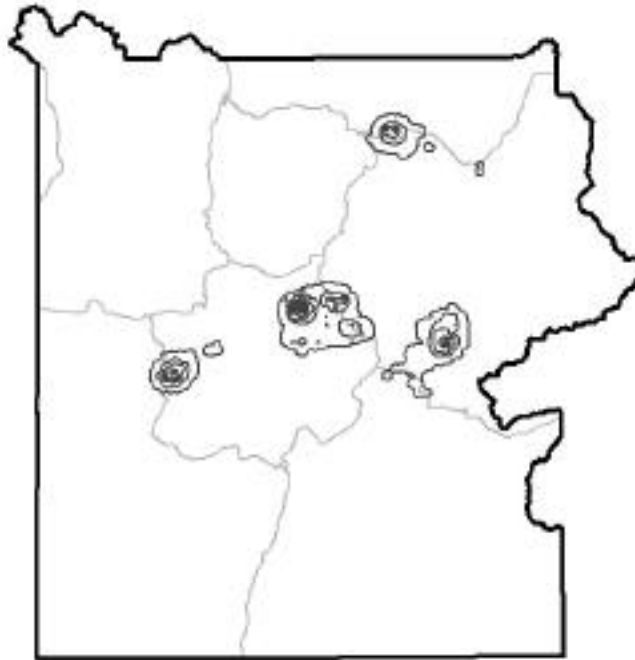


Figure 2. Typical winter distribution in the 1960s and 1970s. The plotted lines indicate contours of proportional use. The outer ring contains 95% of the bison recorded for the flight. Air survey records show only bulls along the lakeshore. Flight 16; date: 14 February 1973; number of bison observed: 702.

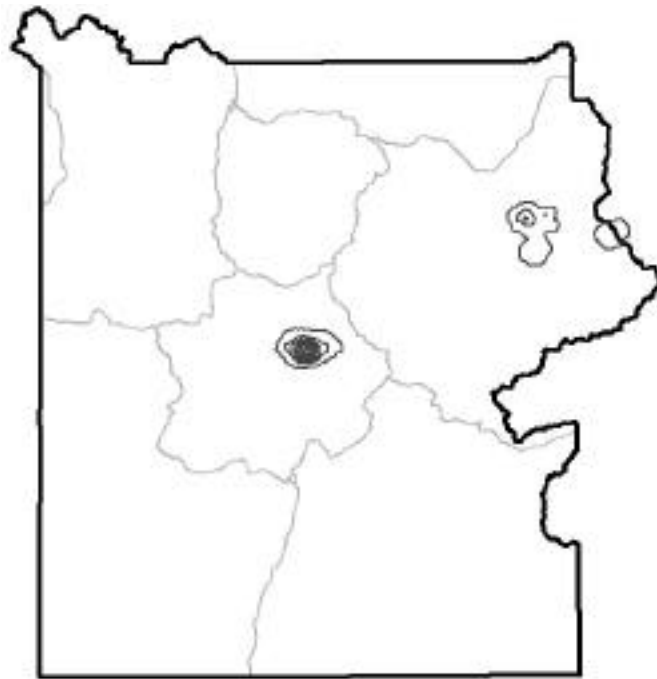


Figure 3. Typical summer distribution in the 1960s and 1970s. The roughly concentric lines indicate proportional use. Note concentration in Hayden Valley and bison presence on the east boundary. Flight 25; date: 29 July 1974; number of bison observed: 832.

season would be underway and the Pelican bison would mix (and interbreed), at least to some extent, with bison from the northern range. Subsequently, groups of bison would recross the Lamar River to the Mirror Plateau. Movements back and forth across the river would continue as the bison utilized various subalpine foraging sites, but they did not stay in the Lamar Valley bottom during spring and summer. Rather they would make large circular movements down and back up, usually spanning 12 to 24 hours. Most of the time they stayed in subalpine areas until storms pushed them down to winter in the lower-elevation valleys of the northern range and Pelican Creek sometime in November. This was the typical land-use pattern that was described for the 1960s (Meagher 1973) and that also prevailed during the 1970s.

In the early 1980s, interior bison land-use patterns began to change. The changes as described here emphasize the bison of the Pelican area, but include the centrally located Mary Mountain (Firehole and Hayden Valley) bison because changes that occurred first on the Pelican winter range appeared to have influenced subsequent changes throughout the interior of the Yellowstone plateau. Generalized descriptive overviews of these bison land-use changes were published earlier (Meagher 1993, 1998; Meagher et al. 1996).

Data Sources

The primary data were derived from 151 aerial surveys of bison numbers and distributions, made from 1970 through July 1997 using a Piper Supercub. The same pilot (Dave Stradley) and observer (Mary Meagher) worked as a team throughout, with rare exceptions for which at least one of those two people was aboard. The data were transferred to a computer, and analyzed as described in Taper et al. (2000). Supplementary ground surveys were made by horseback, foot (skis in winter), and vehicle travel on established park roads. Opportunistic information supplied by park personnel provided additional details. Comparable air and ground methods were used during the 1960s (Meagher 1973).

Bison Land-use Patterns, 1962–1980

In Pelican Valley, bison mixed groups would concentrate initially on sedge foraging areas. As winter progressed, deepening snows eventually closed them out of much of the sedge, and shifts would occur to upland sites, especially the extensive flats above the north side of Pelican Creek, which traverses the length of the valley. Travel trails would develop along south-facing bluff edges and between small hilltops and other accessible forage sites. Usually by the latter part of February, snow depths caused the mixed groups to break into smaller units, sometimes just a few animals, or perhaps a cow with a calf. Commonly, these small groups scattered into widely distributed geothermal sites. Some of these support very limited forage, but there are extensive, interconnected patches of warm, bare ground that allow minimal expenditure of energy (what could be termed a “stand-and-survive” strategy). Warmer parts of major creeks stayed ice- and snow-free and allowed travel and access to creek-bank forage. Some geothermally influenced sites that provided forage also aided travel, including a southward route to the geothermal areas of the lakeshore. Scattered bulls would be found on hilltops, particularly in the western third of the main Pelican Valley, and at various geothermally influenced sites, especially along the shore of Yellowstone Lake east of lower Pelican Creek. Sometimes by late March and early April (while the main valley was still covered with deep snows) mixed groups would move to Mary Bay and nearby geothermal sites. The presence of visible geothermal activity and geothermally influenced foraging sites (with lesser snow depths) appeared to function most years as the survival margin for a bison population in this deep-snow country, especially in late winter (Meagher 1971, 1973, 1976).

As spring developed, forage in geothermal locations in upper Pelican Valley would begin to show new green growth earlier than other places, luring the bison north and east toward the routes used to cross the Mirror Plateau to the subalpine meadows of the upper Lamar area. As the growing season progressed, these bison would move upward to the crest of the Absarokas (Figure 1), usually about the end of July. Thereafter they would make extensive summer range travels that utilized the larger subalpine meadows of both the upper Lamar and the Mirror Plateau.

After the reductions of the 1960s resulted in a park-wide population of

approximately 400 bison (Meagher 1973), a moratorium on management actions allowed an increase in numbers. The bison that wintered in the Lamar Valley of the northern range reached ecological carrying capacity for that locale with the unusually compacted snow conditions that prevailed during the winter of 1975–1976, and expanded their range westward (as they did historically) down the topographic and environmental gradient formed by the Yellowstone River (Meagher 1973, 1989). (*Ecological carrying capacity* is the number of animals that a given area can support under current environmental conditions; see Caughley 1976 and MacNab 1985). Ecological carrying capacity will, of course, change yearly as conditions vary. The centrally located herd that utilized the Mary Mountain locale (Firehole and Hayden Valley combined) continued to increase, as did the winter-isolated Pelican bison. For both winter ranges the use patterns remained within traditional locales, as seen in Figure 2.

Changes in Bison Land-use Patterns, 1980–1997

Changes first began with the bison using the Pelican winter range. On 24 February 1980 (a below-average winter for snowfall in the Pelican area as recorded by the Lake snow course), 332 bison were tallied on that winter range. Of these, 157 were scattered among the relatively barren geothermal sites to the northwest of the main Pelican Valley. This number was unprecedented in those locations compared with prior air surveys. The unbroken snow surface and absence of travel trenches in the main valley suggested that they had been there for some time. Most of the remainder were in other geothermally influenced locations, with one striking exception. For the first time, two mixed groups, containing 13 and 29 bison, were seen on and adjacent to the snow-packed road west of Mary Bay (Figure 1). There was no evidence in the snow of bison movement down Pelican Creek to the road (e.g., of snow texture changes, travel indications that would have been apparent even after a new snowfall). The only travel route showing was that which moved southward out of the main valley to the lakeshore geothermal sites.

For comparison, in an air survey of 28 January 1956, 392 bison were counted for the Pelican winter range (after an early-winter reduction of 118). The winter of 1955–1956 was quite severe, and a review of the flight memorandum (D. Condon, unpublished memorandum, 30 January 1956) showed that the majority of the bison were located at geothermally influenced sites, including 64 at the relatively barren locations northwest of the main valley. Interestingly, only 24 were counted just above the mouth of Pelican Creek, with “some” noted as on the road. (At that time the road was seldom used in winter and the snow was not compacted, although a few park employees wintered at the Lake area and might have made an occasional ski trip to the valley). Also, apparently on 25 January 1956, when Hayden Valley was surveyed, perhaps two dozen bison (mixed group) had created a trail through the deep snow along the east side of the Yellowstone River. According to the pilot (J. Stradley, personal communication), these apparently had traveled from the Pelican area. No such movement from the Pelican area to Hayden Valley was known to be repeated before 1984.

On 22 February 1981 (with there being even less snow than during the preceding below-average winter), 482 bison were counted during the survey of the Pelican-area winter range. Of these, 105 were observed near the mouth of Pelican Creek, which included mixed groups of 14, 23, and 38. Again, there was no evidence in the snow of movement from the main valley southwest down Pelican Creek to the road. In 19 winters of air surveys, this was the first time mixed groups were seen in this location. The circumstances indicated that the bison accessed this location by use of the snow-packed road west from Mary Bay.

With the winter of 1981–1982, both interior bison populations (Mary Mountain and Pelican) reached ecological carrying capacity for the conditions of that winter, which was somewhat above average for snowfall. This was evidenced by an estimated 20% population loss (Meagher 1997), reflecting a recorded natural mortality of over 300 bison.

Continued winter air surveys after 1981 showed ever-increasing numbers of bison in mixed groups located on lower Pelican Creek near the mouth and for 1–1.5 km upstream. From there, Pelican bison winter range use expanded to the Fishing Bridge area and upstream for several kilometers on the east side of the Yellowstone River, and westward across the bridge to meadows in the Lake developed area (Figure 1). By the mid-1980s, it was increasingly apparent that Pelican bison were moving all the way to Hayden Valley during the winter. Occasionally they traveled parallel to the east bank of the Yellowstone River, crossing westward at geothermal sites at the south edge of Hayden Valley. More commonly, however, the snow-packed road that follows the Yellowstone River along the west bank served as the travel linkage between the Fishing Bridge–Lake road junction (Figure 1), and Hayden Valley. Repetitive air surveys indicated that movements occurred throughout the winter.

The Domino Effect

With above-average snow conditions for the winter of 1981–1982, small mixed groups, totaling perhaps 45, were seen at Madison Junction during the air survey of 18 February 1982 (Figure 4). Because the snow-covered road was packed between the Firehole and the junction, no travel trails had to be created through unbroken snow. Once before, during the severe winter of 1955–1956 (as shown by snow course records and narrative written comments by park personnel), perhaps 40–50 bison were known to have moved to meadows west of Madison Junction (Meagher 1973). At that time, none of the snow-covered interior park roads were maintained for travel, and use by people was rare.

After the winter of 1981–1982, with the continued absence of human interference with population numbers, the bison of Hayden Valley were at ecological carrying capacity for prevailing winter conditions. Traditionally, even before that winter, as the season progressed and snows deepened, the greater part of the Hayden Valley bison would cross the Mary Mountain divide to the Firehole, where snow depths were consistently lower. This annual shift would increase the numbers wintering on the Firehole, particularly during the latter part of winter. After Pelican area bison moved to Hayden Valley, thereby increasing numbers

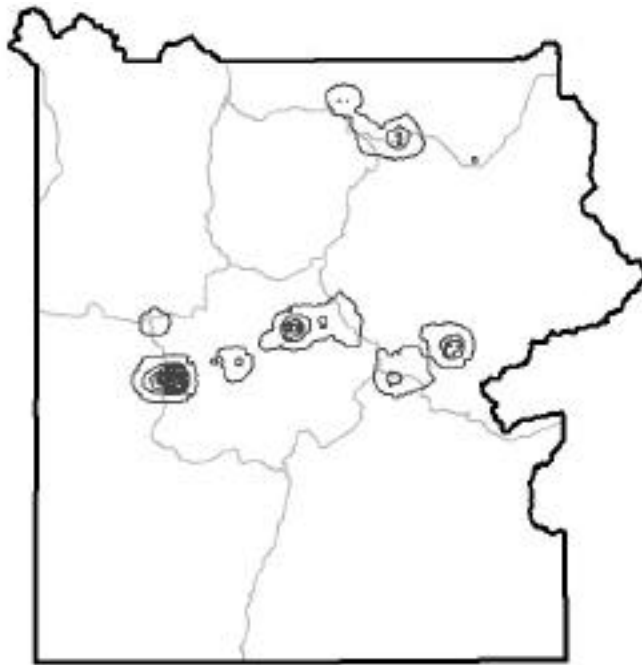


Figure 4. Bison mixed groups at Madison Junction. Note high use on the Firehole. Flight 56; date: 18 February 1982; number of bison observed: 1,907.

there, more bison moved into the Firehole area than would otherwise have been the case. Further, these movements occurred increasingly earlier in the season. Thus, generated by what became an increasing annual winter movement of Pelican bison to Hayden Valley, the distribution and range expansion continued westward (Figure 5). Over time, the interior bison use patterns have shifted westward, with more bison, more of the time, on the Firehole. The movement of Firehole-area mixed groups of bison to Madison Junction that first occurred the winter of 1982 (using the snow-packed road) became an annual occurrence thereafter. And, as more bison moved earlier into the Firehole, more moved earlier, stayed longer, and traveled further west of Madison Junction (Figures 5 and 6). With time, bison mixed groups were commonly seen, even in midsummer, west and north of Madison Junction, and did much shifting between the west side and the Firehole.

Finally, during a few of the winters of the 1990s, bison groups traveled the entire distance from Madison Junction north to Mammoth and the north boundary. During the exceptionally severe winter of 1996–1997, the timing and size of bison removals at boundary areas indicated that between 320 and 350 bison had done this (Taper et al. 2000). Bison have demonstrated a capacity to learn (Meagher 1989), and approximately 30 made this same trip in late October 2000, when the ground was as-yet essentially snow-free along the road corridor. Because the changes that have occurred in interior bison distributions and move-

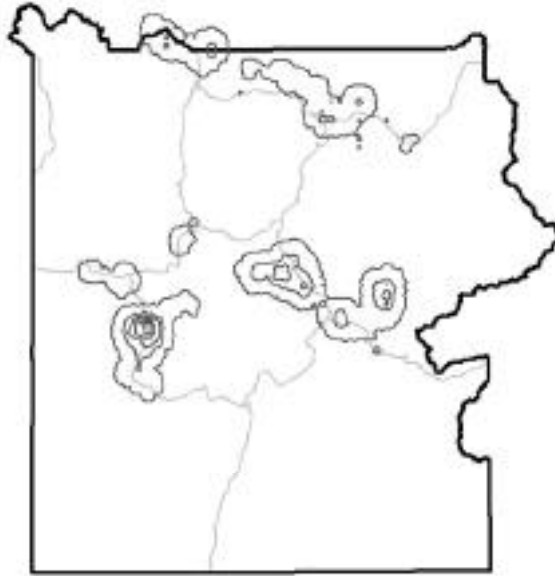


Figure 5. Pelican range expansion merged into Hayden Valley. Note bison west and north of Madison Junction. Flight 71; date: 11 February 1986; number of bison observed: 2,285.



Figure 6. Bison distribution in late February 1996–1997. By this time hundreds had been removed at and outside park boundaries. Flight 145; date: 21 February 1997; number of bison observed: 1,718.

ments apparently began with a west-and-north winter range expansion by Pelican-area bison, and have escalated over the past two decades, we have termed the changes in use patterns *the domino effect*.

Changes in Bison Summer Range Patterns After 1983

The air survey of 21 July 1983 marked the last time bison groups were observed on the crest of the Absarokas south of the head of the Cache-Calfée ridge. Long-term experience indicated that these were probably bison that had come from the Pelican winter range. Some Pelican bison apparently did cross the Mirror Plateau to some of the lower slopes of the Absaroka Mountains during the summer of 1985, but they did not move higher to the crest of the range (D. Stradley, personal communication). Air surveys through the summer of 2001 have not located mixed groups of bison on the east boundary (Taper et al. 2000; J. Mack, personal communication), nor has there been any indication since 1985 that Pelican bison have crossed the Mirror Plateau.

The air survey of 9 August 1984 showed another major change in summer range use. Of 588 bison counted for the northern range unit, 477 were down in the Lamar Valley. These numbers must have included some of the bison that had wintered in the Pelican area, as only 119 bison were located in the subalpine meadows of the Mirror Plateau. This kind of distribution became an annual summer occurrence thereafter.

The seasonal shift of the interior population westward has resulted in enormous summer breeding season congregations of bison in Hayden Valley, sometimes reaching approximately 3,000 animals (Taper et al. 2000). In August, those with affinities for the Pelican winter range would begin to move back to that locale. However, as soon as winter set in, they would start to shift back to Hayden Valley. This seasonal shifting back and forth resulted in larger numbers of bison utilizing interior winter ranges earlier and in greater numbers than had been the pattern prior to the beginnings of winter movement of Pelican bison to Hayden Valley. Preliminary information indicated that this circumstance may be generating habitat degradation in at least some geothermal areas. Four comparative photographs taken from 1912 through 1997 appeared to show directional changes in quantity of vegetative cover that appeared to be supported by the particular characteristics of those soils (Taper et al. 2000).

Pelican-area Winter Use Patterns, 1998–2001

Pelican-area winter use patterns have become very fluid. Prior to the above-observed changes, long-term records suggested that a minimum of approximately 100 bison would remain to survive, regardless of winter severity (Meagher 1971, 1973, 1976). This was evidenced by the winter of 1942–1943 (a recorded 122 bison) and by the comparable winter of 1996–1997, when 94 bison were located in the air survey of 19 May 1997. Because movements from Pelican Valley to Hayden Valley went on throughout the winter, as indicated by decreased numbers with each air survey, the lowest count (minus new calves) in late May and very early June reflected the numbers that spent the entire winter

in the Pelican area. Comparable surveys for May 1998 and 1999 (J. Mack, personal communication) showed some increase, with 145 and 152 counted, respectively.

In contrast, the end-of-winter Pelican-area surveys for 2000 and 2001 (J. Mack, personal communication) dropped to 50 and 47, respectively. For 2000, a detailed review of the Pelican-area survey, coupled with attached map coordinates, allowed scattered bulls that winter in certain sites apart from the rest of the bison to be separated from the total. When both scattered bulls and newly born calves were discounted, only 24 bison were recorded as mixed groups. This is nearly the same as the historically recorded low of 22 in 1902 (Meagher 1973), after cessation of poaching.

Major changes have been observed over the past two decades in the wintering numbers, distribution, and seasonal movements of the bison of the interior of Yellowstone National Park, beginning with those that wintered in Pelican Valley. The analyses of the computerized data from the air surveys of 1970–1997 (Taper et al. 2000) showed changes in bison numbers, distribution, timing of seasonal movements, and social behavior such as group size and cohesiveness. Additional analyses of the habitat data (Jerde et al. 2001) also showed changes in use patterns.

The continued decrease by Pelican-area bison to historic lows that were observed during the winters of 1999–2000 and 2000–2001 reinforce an interpretation that indicates a very fluid and perhaps unstable situation, geographically speaking, in the bison that inhabit the interior of the Yellowstone plateau. Key to this is the long-observed determination of bison to maintain group social bonds if at all possible. Although they can survive by breaking social bonds and scattering into geothermal sites, if presented with a choice they will move preferentially to maintain a higher level of aggregation. They will also shift toward less harsh winter conditions, as is usual with ungulates in mountain habitat. Over time, as this has occurred, many more bison have exited the park in an apparent effort to maintain social aggregations that the within-park habitat would not permit. In so doing, they have come into conflict with different land-use objectives outside the park. Although attempts have been made to force them back into the park, this has been a short-term solution at best, and most have been removed from the population under state legal authority. This situation can be expected to continue.

The data do not provide a cause-and-effect relationship for the observed changes. Interacting factors of environmental fluctuations and bison behavior likely are involved, even as those factors influenced the bison historically. But the air surveys and observational information suggest that another (and also interactive) element may have a role. This is the relatively recent addition of snow-packed travel linkages formed by sections of interior park roads between and within some areas of bison use. The use of snow-packed or plowed roads certainly represents some energy savings to the central herd, and even provides access to areas that would otherwise be inaccessible to bison. It is unclear if these energy savings have merely facilitated a population and range expansion that

would have occurred anyway, or if an apparently minor change has upset a delicately balanced demography and caused the expansion. This raises the possibility that the changes in the bison population and their relationships with their habitat may have a human-caused influence.

The changes appear to be ongoing, and the fluidity of bison shifts suggests that large movements of interior bison across park boundaries likely will occur in the future. These bison probably will be removed from the population. This, coupled with the fluidity of movements and the possibility of habitat changes inside the park, suggests that overall numbers likely will decrease. The summation of the observed changes suggests an uncertain future for the interior park bison.

Acknowledgments

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Mapping the Floor of Yellowstone Lake: New Discoveries from High-Resolution Sonar Imaging, Seismic-Reflection Profiling, and Submersible Studies

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W. J. Stephenson, and S. Y. Johnson

“...we arrived at the summit of the first ridge...It was a pretty steep climb to the top of it, over a volcanic sand composed of broken down obsidian which composed the only rocks around us.”

—Albert Peale, mineralogist,
U.S. Geological Survey, Hayden Survey, August 6, 1871.

Abstract

Recently completed multi-beam sonar-imaging and seismic-reflection surveys of the northern, West Thumb, and central basins of Yellowstone Lake provide insight into post-caldera volcanism and active hydrothermal processes occurring in a large lake environment above a cooling magma chamber. High-resolution mapping of the lake floor reveals an irregular lake bottom covered with dozens of features directly related to hydrothermal, tectonic, volcanic, and sedimentary processes. Newly mapped rhyolitic lava flows that underlie much of Yellowstone Lake exert fundamental control on lake geology, basin bathymetry, and localization of hydrothermal vent sites. Imaged and identified features include over 150 hydrothermal vent sites, several very large (>500 m diameter) and many small hydrothermal explosion craters (~1-200 m diameter), elongate fissures cutting post-glacial (<12 ka) sediments, siliceous hydrothermal spires as tall as 8 m, sublacustrine landslide deposits, deformed lacustrine sediments associated with domal structures and hydrothermal vents, submerged former shorelines, and a recently active graben, all occurring within the southeast margin of the 0.640-Ma Yellowstone caldera. Sampling and observations with a submersible remotely operated vehicle (ROV) confirm and extend our understanding of many of the identified features.

Introduction

Several powerful geologic processes in Yellowstone National Park have contributed to the unusual shape of Yellowstone Lake, which straddles the southeast margin of the Yellowstone caldera (Figure 1). Volcanic forces contributing to the lake's form include the 2.057 ± 0.005 -Ma ($1-\sigma$) caldera-forming eruption of the Huckleberry Ridge Tuff followed by eruption of the 0.640 ± 0.002 -Ma Lava Creek Tuff to form the Yellowstone caldera (Christiansen 1984; Christiansen 2001; Hildreth et al. 1984; U.S.G.S. 1972). A smaller caldera-forming event

about 140 ka, comparable in size to Crater Lake, Oregon, created the West Thumb basin (Christiansen 1984; Christiansen 2001; Hildreth et al. 1984; U.S.G.S. 1972). Large-volume postcaldera rhyolitic lava flows are exposed west of the lake (Figure 1B). Several significant glacial advances and recessions overlapped the volcanic events (Pierce 1974; Pierce 1979; Richmond 1976; Richmond 1977) and helped to deepen the fault-bounded South and Southeast Arms (Figure 1B). More recent dynamic processes shaping Yellowstone Lake include currently active fault systems, erosion of a series of postglacial shoreline terraces, and postglacial (<12 ka) hydrothermal-explosion events, which created the Mary Bay crater complex and other craters.

Formation of hydrothermal features in Yellowstone Lake is related to convective meteoric hydrothermal fluid circulation above a cooling magma chamber. Hydrothermal explosions result from accumulation and release of steam generation during fluid ascent, possibly reflecting changes in confining pressure that accompany and may accelerate failure and fragmentation of overlying cap rock. Sealing of surficial discharge conduits due to hydrothermal mineral precipitation also contributes to over-pressuring and catastrophic failure. Heat-flow maps show that both the northern and West Thumb basins of Yellowstone Lake have extremely high heat flux compared to other areas in the lake (Morgan et al. 1977). Earthquake epicenter locations indicate that the area north of the lake is seismically active (Smith 1991), and ROV studies identify hydrothermally active areas within the lake (Klump et al. 1988; Remsen et al. 1990).

Objectives of this work include understanding the geologic processes that shape the lake and how they affect the present-day lake ecosystem. Our three-pronged approach to mapping the floor of Yellowstone Lake is designed to locate, image, and sample bottom features such as sublacustrine hot-spring vents and fluids, hydrothermal deposits, hydrothermal-explosion craters, rock outcrops, slump blocks, faults, fissures, and submerged shorelines. Chemical studies of the vents indicate that 20 percent of the total deep thermal water flux in Yellowstone National Park occurs on the lake bottom (Morgan et al. 2003). Hydrothermal fluids containing potentially toxic elements (As, Sb, Hg, Mo, W, and Tl) significantly affect lake chemistry and possibly the lake ecosystem. ROV observations indicate that shallow hydrothermal vents are home to abundant bacteria and amphipods that form the base of the food chain, which includes indigenous cutthroat trout, piscivorous exotic lake trout, and grizzly bears, bald eagles, and otters that feed on the potamodromous cutthroat trout during spawning in streams around the lake. Finally, our results document and identify potential geologic hazards associated with sublacustrine hydrothermal explosions, landslides, faults, and fissures in America's premier National Park.

Methods

Yellowstone Lake mapping and sampling conducted in 1999 through 2001 as a collaborative effort between the U.S. Geological Survey, Eastern Oceanics, and the National Park Service (Yellowstone National Park) utilized bathymetric, seismic, and submersible remotely operated vehicle (ROV) equipment as follows.

Figure 1A.

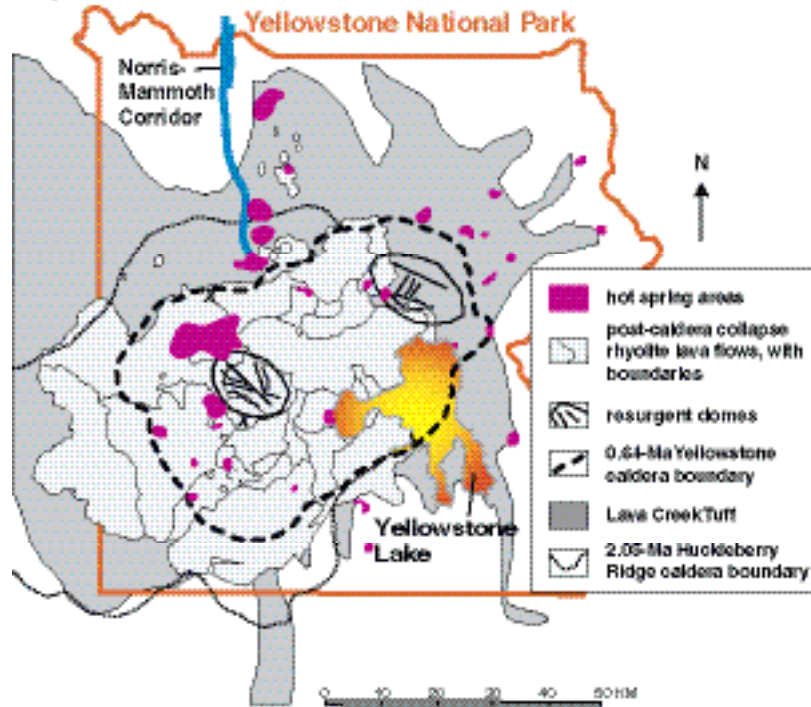


Figure 1B.

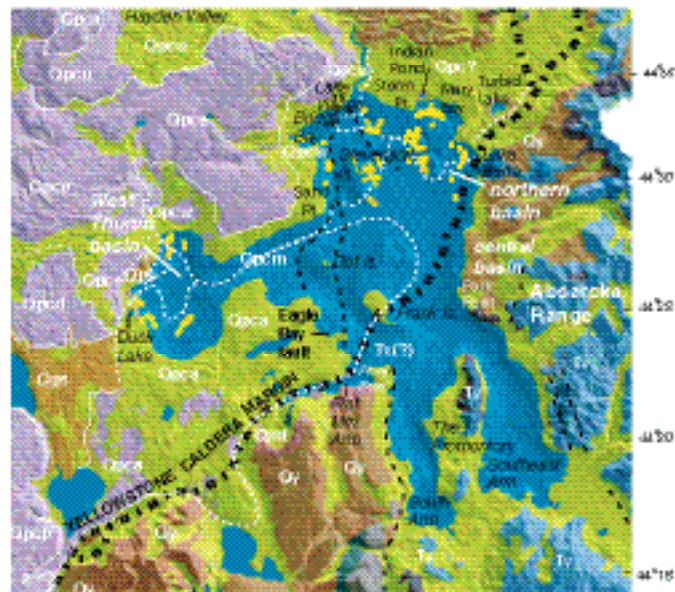


Figure 1. (A) Index map showing the 0.640-Ma Yellowstone caldera, the distribution of its erupted ignimbrite (the Lava Creek Tuff, medium gray), post-caldera rhyolitic lava flows (light gray), subaerial hydrothermal areas (red), and the two resurgent domes (shown as ovals with faults). The inferred margin of the 2.05-Ma Huckleberry Ridge caldera is also shown. Data are from Christiansen 2001. (B) Geologic shaded relief map of the area surrounding Yellowstone Lake in Yellowstone National Park. Geologic mapping is from USGS 1972 and Yellowstone Lake bathymetry is from Kaplinski 1991. Yellow markers in West Thumb basin and the northern basin are locations of active or inactive hydrothermal vents mapped by seismic reflection and multibeam sonar. The lithologic symbols are as follows: Tv = Tertiary volcanic rocks; Qps = tuff of Bluff Point; Qpcd = Dry Creek flow; Qpcm = Mary Lake flow; Qpca = Aster Creek flow; Qpcw = West Thumb flow; Qpce = Elephant Back flow; Qpch = Hayden Valley flow; Qpcn = Nez Perce flow; Qpcp = Pitchstone Plateau flow; Qs = Quaternary sediments (yellow); Qy = Quaternary Yellowstone Group ignimbrites (brown; Christiansen 2001; USGS 1972). Location of Yellowstone caldera margin is from Christiansen 1984, with slight modifications from Finn and Morgan 2002. Funding for the color images printed in this article was provided by the U.S.G.S.

Multi-beam swath-bathymetric surveys were conducted using a SeaBeam 1180 (180 kHz) instrument with a depth resolution of about 1% water depth. Water depth varied from ~4 to 133 m in the survey areas. The multi-beam instrument uses 126 beams arrayed over a 150° ensonification angle to map a swath width of 7.4 times water depth. In the West Thumb basin survey, 99% complete bathymetric coverage was accomplished using the multi-beam system whereas the northern Yellowstone Lake coverage was 95%. Sub-bottom seismic reflection profiling was done with an EdgeTech SB-216S, which sweeps a frequency range from 2 to 16 kHz and has a beam angle of 15–20°. Both the swath unit transducer and the sub-bottom unit were rigidly mounted to the transom of an 8-m aluminum boat used for survey purposes. The Eastern Oceanics submersible ROV is a small vehicle (~1.5 m x 1 m x 1 m) attached to the vessel with a 200-m tether that provides live videographic coverage and remote control of submersible thrusters, cameras, and sampling equipment. This vehicle has a full-depth rating of 300 m and is capable of measuring temperature, conductivity, and depth and of retrieving uncontaminated hydrothermal vent water samples and rock samples up to ~40 cm-long. Previous bathymetric mapping of the lake used a single-channel echo sounder and a mini-ranger for navigation (Kaplinski 1991) requiring interpolation between lines. The new swath multi-beam survey produced continuous overlapping coverage, producing high-resolution bathymetric images and seismic records of the upper 25 m of the lake bottom.

Flow modeling was carried out using the program Basin2, v. 4.0.1, 1982–1999, developed by Craig Bethke, University of Illinois. This program uses finite difference methods to solve Darcy's law for fluids of varying density. The program allows the user to model topographic, compaction-driven, and/or convective flow by setting parameters related to fluid density, heat capacity, heat flow, porosity and permeability. Lava flow schematic shown in Figure 4 modified from (Bonnichsen and Kauffman 1987).

Interpretation of Individual Features

Margin of the caldera: Mapping of Yellowstone Lake has been primarily in the 0.64-Ma Yellowstone caldera but it was not until the central basin was mapped that the margin of the caldera was identified, here as a series of elongate troughs. Geologic maps show the margin of the Yellowstone caldera entering the western part of Yellowstone Lake at the entrance to Flat Mountain Arm and resurfacing north of Lake Butte (Figure 1B). The location of the caldera margin between these points has had various interpretations, based primarily on lower resolution bathymetry. Previous interpretations include a margin trending north of Frank Island as well as an inferred margin south of Frank Island. Based on new data, we infer the margin of the Yellowstone caldera to pass through the southern part of Frank Island.

High-resolution aeromagnetic maps (Finn and Morgan 2002) of Yellowstone Lake show a series of discontinuous moderate amplitude negative magnetic anomalies in the southeast part of the central basin (Figure 2A). These anomalies coincide with bathymetric lows as identified in the new sonar image mapping. Careful examination of the bathymetry on Figure 3 shows these lows to extend as a series of elongated troughs northeast from Frank Island across the deep basin of the lake. Similar, though somewhat smaller, troughs emerge on the western side of Frank Island and continue toward the head of Flat Mountain Arm. Here, the caldera margin separates Tertiary andesitic rocks and pre-caldera and caldera rhyolitic rocks to the south from young, post-caldera rhyolites to the north and northwest.

Examination of the reduced-to-the-pole aeromagnetic map shows pronounced positive magnetic anomalies over the Absaroka Range along the eastern side of Yellowstone Lake (Figure 2A). Rugged topographic relief and predominantly highly magnetized rock give the area its high positive magnetic character. Similarly magnetized material occurs along Promontory Point where Tertiary andesitic lava and debris flows are prominently exposed in cliffs several hundred meters thick. The magnetic signature is repeated north and east of Plover Point in southern Yellowstone Lake and along the eastern shore of the lake near the outlet for Columbine Creek. Finn and Morgan (2002) suggest that this series of positive magnetic anomalies are caused by Tertiary volcanic rocks at the surface, as exposed at Promontory Point and in the Absaroka Range, or buried at shallow depths in the lake, such as north of Plover Point northward into the southern third of Frank Island or due west along the eastern shore (Figure 2A).

From west to east, we interpret the margin of the caldera within the lake to pass in a general eastern direction following Flat Mountain Arm, then northeastward cutting through the southern part of Frank Island, and then again north-eastward (Figure 3). The amplitudes of magnetic anomalies on the northern part of Frank Island are similar in character as those associated with postcaldera rhyolitic lava flows, such as much of the West Thumb, Hayden Valley, or Aster Creek flows (Figure 2A). In contrast, the amplitude of the magnetic anomaly on the southern side of the island is steeper of greater magnitude and similar to that seen in the Absaroka or Promontory Point. This location of the caldera margin

based on mapped geology on land and the series of magnetic anomalies in the lake is consistent with the recently acquired bathymetry (Figures 1, 2, 3).

Rhyolitic lava flows: A major discovery of the surveys is the presence of previously unrecognized rhyolitic lava flows on the floor of the lake. The lava flows are key to the control of many geologic and hydrologic features in the lake.

Areas of the lake bottom around the perimeter of West Thumb basin (Figure 3) have steep, nearly vertical margins, bulbous edges, and irregular hummocky surfaces. Seismic-reflection profiles in the nearshore areas of West Thumb basin show high-amplitude reflectors beneath about 7–10 m of layered lacustrine sediments (Figure 4A). We interpret these sublacustrine features to be buried rhyolitic lava flows that partly fill the interior of the 140-ka West Thumb caldera. Subsequent sampling with the submersible ROV collected rhyolite from an inferred lava-flow area in east-central West Thumb basin.

In the northern and central basins, similar features also are present. Sublacustrine rhyolitic lava flows in the northern and northeastern areas of the northern basin are inferred from the bathymetry and do not have mapped sub-aerial equivalents. These features also could represent shallow rhyolitic intrusions. A dominant lithic clast present in the hydrothermal explosion breccia of Mary Bay and prevalent in the alluvium of the lower Pelican Valley (Figure 1B) is a quartz-rich porphyry that has not been described before. These porphyry clasts may be derived from a buried volcanic unit in the lower Pelican Valley that may be producing the moderate positive magnetic anomaly seen here (Finn and Morgan 2002) (Figure 2).

Large-volume rhyolitic lava flows (10's of km³) on the Yellowstone Plateau control much of the local hydrology. Stream drainages tend to occur along flow boundaries, rather than within flow interiors. Characteristic lava-flow morphologies include near-vertical margins (some as high as 700 m), rubbly flow carapaces, hummocky or ridged tops, and strongly jointed interiors. Spherulitic and lithophysal zones commonly include large cavities. Many flows have vitrophyric exterior rinds with shrinkage cracks and sheet-jointed crystallized interior zones. Breccias occur locally.

In many exposures of postcaldera rhyolite lava flows near the current margins of Yellowstone Lake, including West Thumb basin, and north of the lake in Hayden Valley, ample evidence exists for interaction between emplacement of hot rhyolitic lava flows and standing water. Clastic dikes, highly fractured perlitic vitrophyre, massive rhyolitic breccias with fine-grained and altered matrix, and entrained stream, beach, and lake sediments point to emplacement of lavas in an aqueous environment.

Magnetic signature of rhyolitic lava flows: Comparison of the new high-resolution aeromagnetic maps (Finn and Morgan, 2002) (Figure 2) with geologic maps (Figure 1B) (Blank 1974; Christiansen 1974; Christiansen and Blank 1975; Richmond 1973) shows a close relationship of magnetic anomalies to the mapped individual lava flows. Moderate-amplitude positive magnetic anomalies coincide with the mapped extent of subaerial post-caldera rhyolitic lava flows (Finn and Morgan 2002) and extend into the sublacustrine environment in many

Figure 2A.

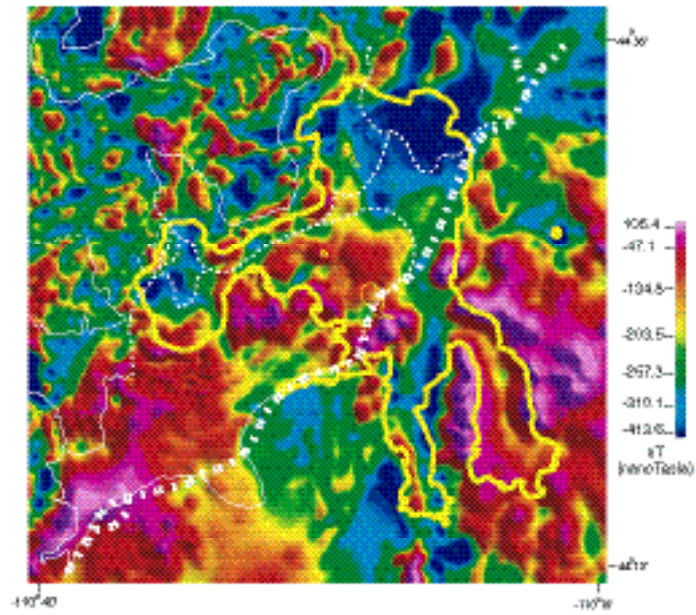


Figure 2B.

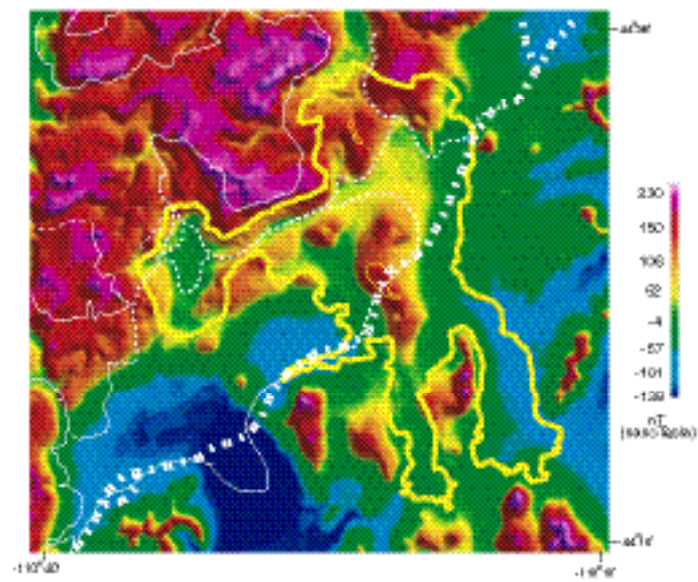


Figure 2. (A) Color shaded-relief image of high-resolution, reduced-to-the-pole aeromagnetic map (Finn and Morgan 2002). Sources of the magnetic anomalies are shallow and include the post-caldera rhyolite lava flows (some outlined in white), which have partly filled in the Yellowstone caldera. Commonly, rhyolitic lava-flow margins have impermeable glassy rinds that are not subject to hydrothermal alteration, producing distinctive positive magnetic anomalies. Extensive areas of negative magnetic anomalies in the West Thumb and northern basins and along the caldera margin northeast of the lake are areas of high heat flow and intense present and past hydrothermal alteration, as suggested by sublacustrine vent locations (Figure 1B). (B) Color-shaded relief image of the magnetic anomaly due to uniformly magnetized terrain in the present Earth's field direction of inclination = 70° and a declination of 15° with an intensity of 2.5 A/m, and then reduced to the pole (Finn and Morgan 2002). Rhyolitic lava flows (outlined in white) underlying Yellowstone Lake are shown clearly on this map.

areas (Figures 1, 2, 3). For example, northwest of the northern lake basin, moderate-amplitude magnetic anomalies correspond to mapped subaerial postcaldera rhyolitic lava flows (Figure 1B) and extend from land into the lake (Figure 2A). Similarly, mapped subaerial lava flows around West Thumb basin and west of the central lake basin can be extended into the lake based on moderate amplitude positive magnetic anomaly patterns (Figure 2). These characteristic magnetic signatures, in combination with the new bathymetric and seismic data, allow identification and correlation of rhyolitic lava flows well out into the lake.

In the northern basin, negative magnetic anomalies (Figure 2A) are extensive. Excessively high heat flow in the Mary Bay area (1,550–15,600 mW/m²) (Morgan et al. 1977), in part related to proximity to the margin of the Yellowstone caldera, indicates that hydrothermal activity has destroyed or significantly reduced the magnetic susceptibility of minerals in rocks and sediments producing the observed negative magnetic anomalies. Comparison of the reduced-to-the-pole magnetic anomalies (Figure 2A) with those caused by uniformly magnetized terrain (Figure 2B) draws attention to areas, such as in the northern basin at Mary Bay or near Stevenson Island, with buried magnetic sources or places where the surficial lava flows are not as magnetic or are thinner than expected. While the shape of the observed magnetic anomaly mimics that caused by terrain, the amplitudes of the anomalies are different, possibly implying that topography contributes to the observed anomaly but has a magnetization different than calculated. In this case, we interpret the topography as representing large, unidentified rhyolitic lava flows.

Variations in total field magnetic intensity and susceptibility (Finn and Morgan 2002) appear to correspond, in part, to the degree of alteration present in the rhyolite that produces the anomaly. In many exposures where a flow is glassy, flow-banded, and fresh, such as the West Thumb rhyolite flow due west of the Yellowstone River (Figures 2A, 3), the magnetic anomaly of the exposure generally appears as positive. In contrast, in many exposures where evidence for emplacement of the flow into water or ice is present, such as the West Thumb rhyolite flow exposed on the northeast shore of West Thumb basin (Figures 2A, 3), the magnetic anomaly is negative (Figure 2A). All of the postcaldera rhyolites have a normal magnetic remanence, being emplaced during the past 160 ka



Figure 3. High-resolution multibeam sonar imaging and seismic mapping of the northern basin was completed in 1999, of West Thumb basin in 2000, and of the central basin in 2001. (A) Index map using the new high-resolution bathymetric map, shown as colored contoured intervals, of the West Thumb, northern, and central basins of Yellowstone Lake, acquired by multibeam sonar imaging and seismic mapping, surrounded by gray-shaded relief DEM. (B) New high-resolution bathymetric map, showed as blue shaded relief map, of the West Thumb, northern, and central basins of Yellowstone Lake, acquired by multibeam sonar imaging and seismic mapping, surrounded by colored geologic map of the area around Yellowstone Lake. The new maps show previously unknown features such as a ~500-m-wide hydrothermal-explosion crater (east of Duck Lake), a 500-m explosion crater south of Frank Island, numerous hydrothermal vents, fissures, submerged lakeshore terraces, and inferred rhyolitic lava flows that underlie 7 to 10 m of post-glacial sediments in West Thumb basin. In the northern basin, large hydrothermal-explosion craters in Mary Bay and south-south-east of Storm Point, numerous smaller craters related to hydrothermal vents, landslide deposits along the eastern margin of the lake near the caldera margin (Figure 1), and post-caldera rhyolitic lava flows form the landscape of the northern basin. Fissures west of Stevenson Island and the graben north of Stevenson Island may be related to the young Eagle Bay fault (see Figure 1B). Subaerial lithologies include Quaternary sediments (= Qs), hydrothermal deposits (= Qh), hydrothermal explosion breccia deposits (= Qhe), tuff of Bluff Point (= Qps), Elephant Back flow (= Qpce), Dry Creek flow (= Qpcd), West Thumb flow (= Qpcw), Lava Creek Tuff (= Qyl), Tertiary Langford Formation volcanics (= Tl), and Tertiary Langford Formation intrusives (= Thi) (USGS 1972).

(Christiansen 2001); thus, susceptibility is the primary variable and ranges from 10^{-3} for relatively pristine rocks to 10^{-6} for extensively hydrothermally altered rocks (Finn and Morgan 2002).

Rhyolitic lava flows control geothermal activity: The floor of Yellowstone Lake, two-thirds of which is within the Yellowstone caldera, lies above a large cooling magma chamber (Eaton et al. 1975; Fournier 1989; Fournier et al. 1976; Lehman et al. 1982; Stanley et al. 1991; Wicks et al. 1998). The new high-resolution bathymetry of the northern, central, and West Thumb basins of Yellowstone Lake shows that many hydrothermal features in the surveyed areas are located within or along edges of areas of high relief, interpreted as rhyolitic lava flows (Figures 1B, 3). Based on our observations of the abundant present-day distribution of hydrothermal vents (Figures 1B, 3), we infer that the rhyolitic lava flows act as a cap rock exerting influence on the flow of thermal water. Upwelling hydrothermal fluids are focused preferentially through the basal breccia deposits and fractures of the rhyolitic lava flows whereas hydrothermal fluids conducted through lake and glacial sediments tend to be more diffuse (Figure 5A).

In order to evaluate the effect of rhyolitic lava flows on convective fluid flow in the sublacustrine environment, a pair of simple two-dimensional flow models was constructed (Figure 5B, C). The first model involves fluid flow in a sediment volume 1-km thick by 10-km wide (Figure 5B) covered by lake water 200 m deep. Both left and right edges of the sediment volume are open to flow. Vertical-direction (z) permeability is 0.001 darcy and horizontal-direction (x) permeability is 0.01 darcy, properties expected for lacustrine or glacial sediments. In order to simulate a magma chamber at depth, heat flow through the base of

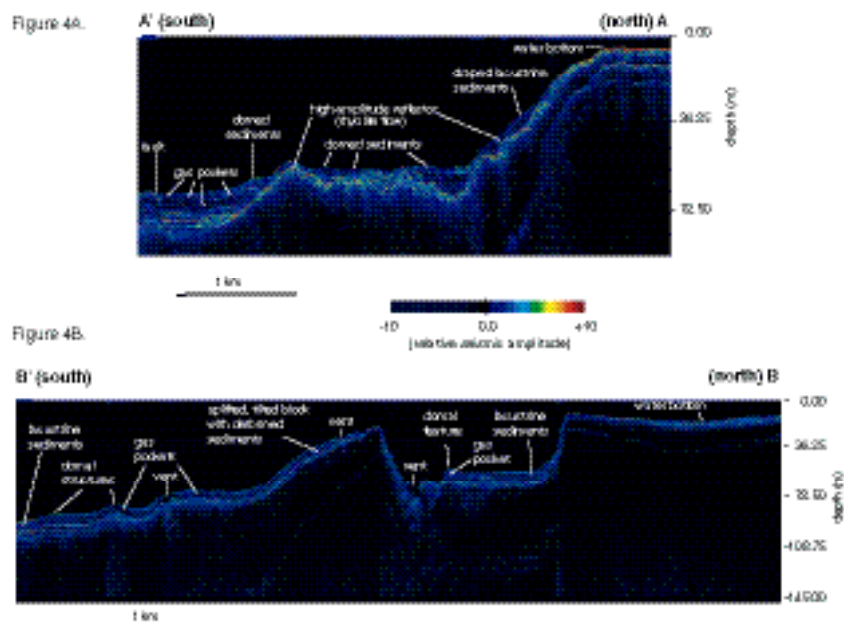


Figure 4. (A) High-resolution seismic-reflection image from northwestern West Thumb basin showing high-amplitude (red) reflector interpreted as a sub-bottom rhyolitic lava flow. Glacial and lacustrine sediments, marked in blue, overlie this unit. The data amplitudes have been debiased and spatially equalized only. No additional gain corrections or filtering are applied. (B) High-resolution seismic-reflection image (line YL72) across part of Elliott's explosion crater, showing small vents, gas pockets, and domed sediments in the lacustrine sediments that overlie the crater flank. Lacustrine sediment thickness in the main crater indicates 5,000–7,000 years of deposition since the main explosion. More recent explosions in the southern part of the large crater ejected post-crater lacustrine sediments and created new, smaller craters and a possible hydrothermal siliceous spire. Lava flow schematic modified from Bonnicksen and Kauffman 1987.

the section is set at 4 HFU or about 167.6 mW/m^2 ($1 \text{ heat flow unit} = 10^{-6} \text{ cal/cm}^2/\text{sec} = 41.9 \text{ mW/m}^2$), much higher than a typical continental value of $40\text{--}70 \text{ mW/m}^2$. Results indicate uniform increase of temperature with depth, recharge at the surface, flow out both ends, and flow rates of $<1 \text{ mm/yr}$. The basal heat flow value used in these calculations produces the highest possible thermal gradient without violating the assumptions of the modeling approach (boiling not allowed, fluid density and viscosity extremes not allowed, fluid temperature $<300^\circ\text{C}$).

Addition of a sublacustrine 200-m-thick cap rock, in this case a fully cooled lava flow, on top of the model sedimentary section (Figure 5C) produces dramatic changes in fluid flow. The lava flow is assigned permeabilities of 0.02 darcy in the z-direction and 0.045 darcy in the x-direction, within the range measured for fractured volcanic rocks. Results indicate that a thick cap rock, in

this case a sublacustrine lava flow, atop the sediment causes localization of intense thermal upflow through the lava flow and strong discharge at the surface of the flow. Fluid flow rates in the model range up to 160 mm/yr and temperatures to $>130^{\circ}\text{C}$. In the natural situation, localization of upflow is expected along fracture zones, producing focused hydrothermal vents. Field observations and this physical model may explain the preferential distribution of hydrothermal vents and explosion craters located within or at the edges of rhyolitic lava flows in Yellowstone Lake.

Large hydrothermal explosion craters: Large (>500 m) circular, steep-walled, flat-bottomed depressions are mapped at several sites in the West Thumb, central, and northern lake basins (Figures 3, 5) and are interpreted as large composite hydrothermal explosion craters. A newly discovered 500-m-wide sublacustrine explosion crater in the western part of West Thumb basin near the currently active West Thumb geyser basin is only 300 m east of Duck Lake (Figure 3), a postglacial (<12 ka) hydrothermal explosion crater (Christiansen 1974; Christiansen 2001; Richmond 1973; U.S.G.S. 1972). Here, heat-flow values are as high as 1500mW/m^2 (Morgan et al. 1977) and reflect the hydrothermal discharge that contributed to the formation of this explosion crater. The 500-m-wide West Thumb explosion crater is surrounded by 12- to 20-m high nearly vertical walls and has several smaller nested craters along its eastern edge. These nested craters are as deep as 40 m and have more conical forms reflecting their younger ages relative to the main crater. Temperatures of hydrothermal fluids emanating from the smaller northeast nested crater have been measured at 72°C by ROV.

In the northern basin of Yellowstone Lake, Mary Bay represents a roughly 1-km by 2-km area of coalesced explosion craters (Morgan et al. 1998; Wold et al. 1977) (Figure 3) in an area of extremely high heat flow (Morgan et al. 1977). Radiocarbon dates from charcoal in and carbonized soils below the ejected breccia deposit exposed in the wave-cut cliffs along the shore of Mary Bay indicate that eruption of this crater occurred at 10.8 ka (Morgan et al. 1998). Detailed stratigraphic measurements of the breccia deposit indicate that multiple explosions and emplacements occurred during formation of this large and complex feature. Submersible investigations show that hydrothermal vent fluids from a 35-m-deep crater in the Mary Bay complex have temperatures near the 120°C limit of the temperature probes.

One kilometer southwest of the Mary Bay crater complex is another large (~ 800 m diameter) composite depression we informally refer to as Elliott's Crater (Figure 6), named after Henry Elliott who helped map Yellowstone Lake in the Hayden survey (Merrill 1999) in 1871. Development of Elliott's explosion crater is best illustrated in a north-south seismic reflection profile (Figure 4B). Zones of non-reflectivity in the seismic profile on the floor and flanks of the large crater are probably hydrothermally altered and possibly heterolithologic explosion-breccia deposits, similar in character to those exposed on land and associated with subaerial explosion craters. Seismic profiles of the hummocky area southeast of Elliott's crater also are non-reflective and may represent a layer of

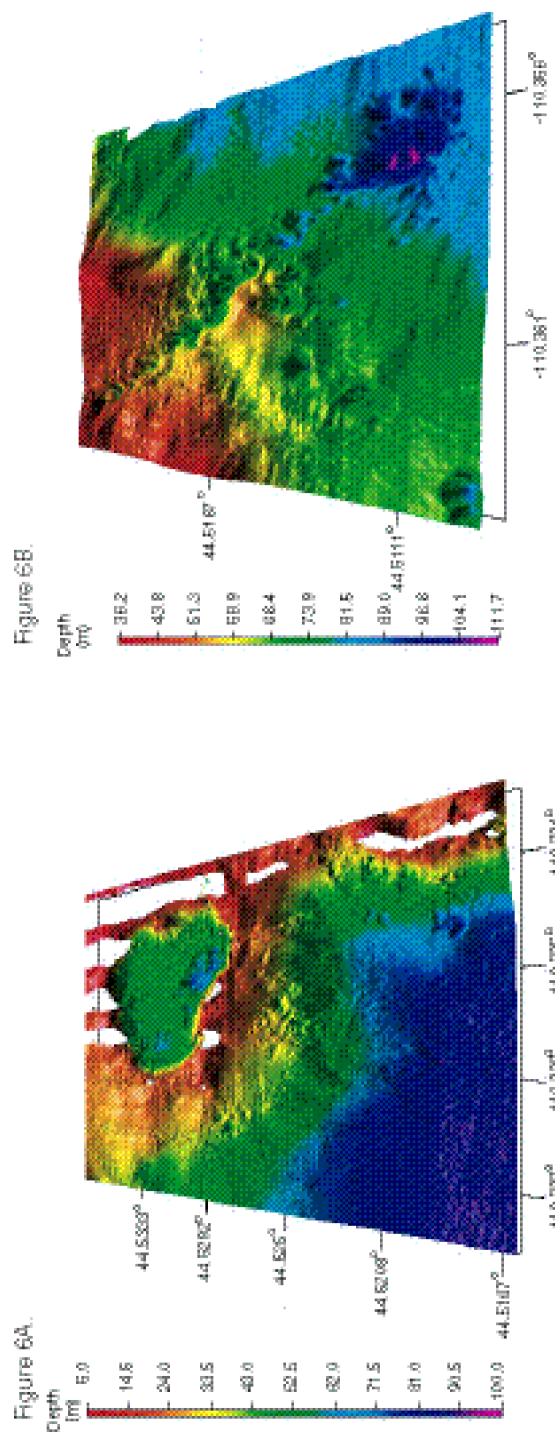
Figure 5. (A) Schematic diagram showing physical features of a rhyolitic lava flow (modified from Bonnicksen and Kauffman 1987). (B) Fluid-flow model with simple sandstone aquifer (no caprock), which results in low flow velocities, recharge at the surface, and lateral flow out of both ends of the model aquifer. Even though heat flow is the same as in (C), subsurface temperatures in this model never exceed 110°C and strong convection cells are not established. (C) Fluid-flow model with a fully cooled rhyolitic lava flow acting as caprock. The underlying sandstone aquifer and heat flow are exactly the same as in (B). The addition of a 200-m-thick fractured crystalline rock cap strongly focuses the upward limb of an intense convection cell under the caprock. In this model, fluid temperatures reach 130°C, and flow velocities are 100 times higher than in the uncapped aquifer (B).

heterolithic and/or hydrothermally altered material erupted from this crater.

Following the initial major explosive event, lacustrine sediments, imaged as laminated reflective layers in the seismic profile (Figure 4B), accumulated in the floor of the crater and on its south flank. Opaque zones within the stratified sedimentary fill of the crater indicate the presence of gas. The presence of two V-shaped vents at the south end of the crater floor further indicates recent hydrothermal activity within the explosion crater. Two additional hydrothermal vents imaged in Figure 4B occur on the south flank, outside of the crater. These vent areas differ slightly in morphology from the nested vents within Elliott's Crater. These flank vents may have formed by collapse resulting from vigorous hydrothermal activity, extensive hydrothermal alteration, and structural failure of the overlying cap rock.

The seismic profile shows about 80 m of vertical relief between the current lakeshore and the average depth of the deeper lake basin several km south of Mary Bay (Figure 4B). We attribute most of this elevation difference to morphology associated with a previously unrecognized lava flow or shallow rhyolite intrusion present but unexposed in lower Pelican Valley (Figure 1A) and extending into Mary Bay, as discussed above. Slightly less than 10 meters of vertical difference in rim height is observed in the seismic profile of the explosion crater between the northern and southern rims. This nearly 10 meter difference may represent doming associated with hydrothermal activity. A currently active example of hydrothermal doming on a much smaller scale can be seen on the southern flank of the large explosion crater (Figure 4B). Here, a seismically opaque area interpreted as a large pocket of gas, probably steam, is present at shallow (<8 meters) depth below the sediment-water interface. Laminated lacustrine sediments show a slight convex-upward doming above this gas pocket that we attribute to uplift. Figure 4B also shows an area on the southern flank where we suggest that a gas pocket breached the surface and is now a hydrothermal vent. Note the attitude of the reflective layers dipping into and draping over the rim of the vent.

Hydrothermal explosions have occurred repeatedly over the past 12 ka in Yellowstone National Park and are primarily confined within the boundaries of the Yellowstone caldera (Figure 1). We interpret the large sublacustrine depressions as post-glacial hydrothermal-explosion craters similar in origin to those on land, such as Duck Lake, Pocket Basin, the 8.3-ka Turbid Lake crater, and the 3.0-ka Indian Pond crater (Figure 3) (Morgan et al. 1998; Muffler et al. 1971; Wold et al. 1977). In



contrast to the subaerial craters, which have radial aprons of explosion breccia ejected during crater formation (Hamilton 1987; Love and Good in press), many of the sublacustrine circular depressions lack an obvious apron. This may indicate either more widespread dispersal of ejection deposits in the lake or that some process, such as collapse associated with hydrothermal alteration, created those depressions.

Small hydrothermal explosion craters on the floor of Yellowstone Lake:

Seismic-reflection profiles of the surveyed areas in the northern and West Thumb basins of Yellowstone Lake reveal a lake floor covered with laminated lacustrine muds and diatomite, many of which are deformed, disturbed, and altered. High-resolution bathymetric mapping reveals that many of these areas contain small (<20 m) depressions pockmarking the lake bottom (Figures 3, 6B). In seismic-reflection profiles (Figure 4B), these features typically are imaged as V-shaped structures associated with reflective layers that are deformed or have sediments draped across their edges. Areas of high opacity or no reflection occur directly beneath these features and are interpreted as gas pocket, or hydrothermally altered zones. Evidence for lateral movement of hydrothermal fluids is seen beneath and adjacent to many of these features in seismic-reflection profiles as areas of high opacity or no reflection and in the high-resolution aeromagnetic data as areas of low magnetic intensity which represent a much larger area than seen in the surficial hydrothermal vents (Finn and Morgan 2002). Associated with these vent areas are smaller domal structures in which the laminated diatomaceous lacustrine sediments have been domed upward as much as several meters by underlying pockets of gas, presumably steam.

We interpret these features as sublacustrine hydrothermal vents with associated hydrothermal feeders. We attribute much of the deformation and alteration to hydrothermal vent channelways and subsurface migration of hydrothermal fluids. In contrast, areas devoid of inferred hydrothermal vents show well-laminated seismic reflections characteristic of lake sediments. Over 150 vents have been mapped in the northern lake basin. Several thermal fields also are identified in West Thumb basin including a large northeast-trending thermal-vent field in the southeast, another field in the northwest, and several in the west (Figure 3). These fields contain dozens of small hydrothermal vents.

Siliceous spires: Siliceous spires occur in Bridge Bay (Figure 3) in the northern basin of Yellowstone Lake, discovered in 1997 by Eastern Oceanics and the University of Wisconsin-Milwaukee. Approximately 12–15 spires are identified in water depths of ~15 m. These roughly conical structures (Figure 7A) are up to 8 m in height and up to 10 meters wide at the base. A small 1.4-m-tall spire collected from Bridge Bay in cooperation with the National Park Service on 1999 shows the spire base to be relatively shallow (~0.5 m below the sediment-water interface), irregular, and rounded; spire material above the sediment-water interface constitutes about 75% of the entire structure. The sediment-water interface is recorded on the spire as a zone of banded ferromanganese oxide-stained clay-rich and diatomaceous sediments. Below the sediment-water interface, the spire is non-oxidized. Above the interface, the spire has a dark reddish-brown oxide

coating (Figure 7B). The interior of the collected spire is white, finely porous, and has thin (from 0.3 cm to <3 cm diameter), anastomosing vertical pipe-like structures through which hydrothermal fluids flowed. Little oxide is found in the interior of the spire structure but oxidation surfaces are present on former growth fronts (Figure 7B). Chemical and oxygen-isotope analyses, and scanning electron microscope (SEM) studies of the spires show them to be composed of silicified bacteria, diatom tests, and amorphous siliceous sinter associated with sub-lacustrine hydrothermal vent processes (Figure 7C). The Bridge Bay spires are strongly enriched in As, Ba, Mn, Mo, Tl, Sb, and W (Figure 7D). Oxygen isotopic ratios suggest formation at about 70–90°C. U-series disequilibria dating of two samples from one spire both yield a date of about 11 ka (ages were determined by Neil Sturchio, written communication, 1998); thus, the spires are immediately postglacial. Spires may be analogous in formation to black-smoker chimneys, well-documented hydrothermal features associated with deep-seated hydrothermal processes at oceanic plate boundaries (Delaney et al. 2001).

Landslide deposits: Multibeam bathymetric data reveal hummocky lobate terrain at the base of slopes along the northeast and eastern margin of the lake basin (Figure 3). Seismic-reflection data indicate that the deposits range in thickness from 0–10 m at the eastern edge of the lake and become thinner toward the interior of the lake basin. We interpret these as landslide deposits. Proximal deposits at the eastern lake edge are as thick as 10 m near the shore. The distal landslide deposits are much thinner and extend as far as 500 m into the deeper lake basin. The thickness of the lacustrine-sediment cap deposited above the landslide deposits varies and suggests that the landslides were generated by multiple events. We think it is likely that they were triggered by ground shaking associated with earthquakes and (or) hydrothermal explosions. The eastern shore of Yellowstone Lake, near where these landslide deposits occur, marks the margin of the Yellowstone caldera (Christiansen 1984; Christiansen 2001; Hildreth et al. 1984; U.S.G.S. 1972) and abuts steep terrain of the Absaroka Mountains to the east, both possible factors contributing to the landsliding.

Submerged shorelines: Several submerged former lake shorelines form underwater benches in the West Thumb and northern basins of Yellowstone Lake (Figure 3). The submerged, shallow margins (depth <15–20 m) of the northern basin are generally underlain by one to three relatively flat, discontinuous, post-glacial terraces that record the history of former lake levels. Correlation of these submerged shoreline terraces around the lake is based primarily on continuity inferred from multibeam bathymetric data and shore-parallel seismic-reflection profiles. These data indicate that lake levels were significantly lower in the past. An extensive bench occurs south of Steamboat Point and along the west shore of the northern basin south of Gull Point. In Bridge Bay, submerged-beach pebbly sand 5.5 m below the present lake level yielded a carbon-14 date of $3,560 \pm 60$ yr B.P. (Pierce et al. 1997). Well-developed submerged shoreline terraces are present in West Thumb basin, especially along the southern and northern edges.

Relief on these terraces is as much as 2–3 m, a measure of post-depositional vertical deformation. Documentation of the submerged terraces adds to a data-

Mapping the Floor of Yellowstone Lake

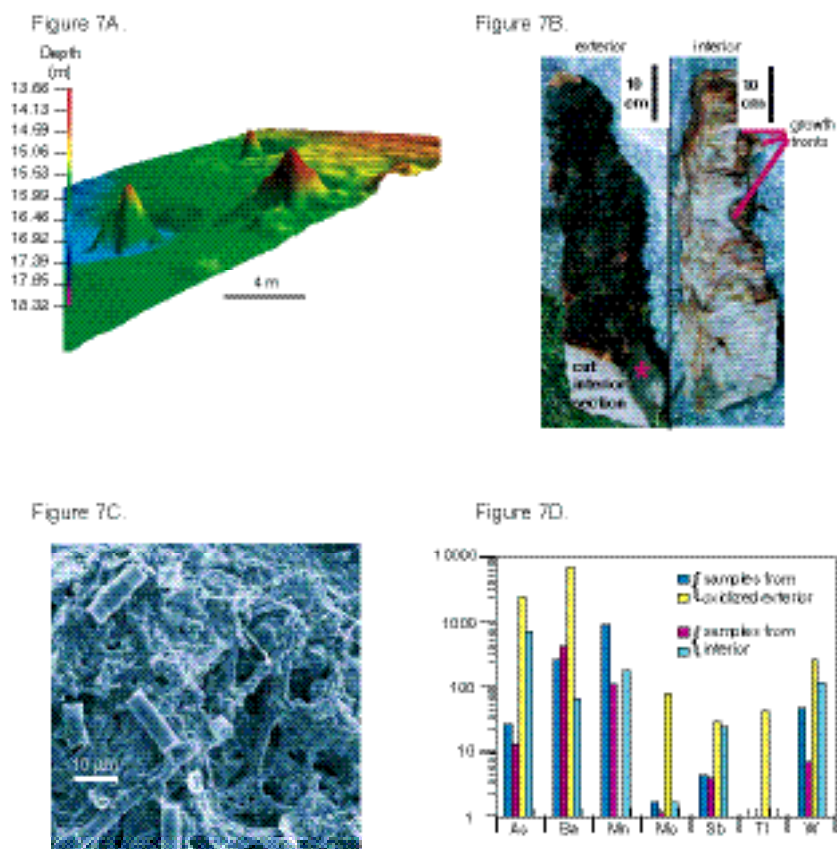


Figure 7. (A) Bathymetric image of spires in Bridge Bay, showing roughly conical shapes. Roughly a dozen such siliceous sinter spires occur near Bridge Bay, some as tall as 8 m. Many of the spires occupy lake-bottom depressions (possible former explosion or collapse craters). (B) Photographs of the exterior and interior of a 1.4 m-tall spire sample recovered from Bridge Bay by National Park Service divers. The sediment–water interface of this spire is apparent near the base of the exterior section, as seen in the dramatic change in color in the outer rind of red-brown ferromanganese oxide to the light gray interior. (The red asterisk on the photograph showing the exterior is on a natural external surface of the spire below the sediment–water interface.) Former growth fronts on the spire can be seen as shown in the photograph of the interior section. (C) SEM image of diatoms, silicified filamentous bacteria, and amorphous silica from a spire sample. (D) Summary bar graph of chemical analyses of spire samples showing substantial concentrations of potentially toxic elements: arsenic, barium, manganese, molybdenum, antimony, thallium, and tungsten.

base of as many as 9 emergent terraces around the lake (Locke and Meyer 1994; Locke et al. 1992; Meyer 1986; Pierce et al. 1997). Changes in lake level over the last 9,500 radiocarbon years have occurred primarily in response to episodic uplift and subsidence (inflation and deflation) of the central part of the Yellowstone caldera (Dzurisin et al. 1994; Pelton and Smith 1982; Pierce et al.

1997; Wicks et al. 1998). Holocene changes in lake level recorded by these terraces have been variably attributed to intra-caldera magmatic processes, hydrothermal processes, climate change, regional extension, and (or) glacioisostatic rebound (Dzurisin et al. 1994; Locke and Meyer 1994; Meyer and Locke 1986; Pierce et al. 1997; Wicks et al. 1998).

Fissures and faults: Features identified in the western area of the northern and central basins (Figure 2B) include a set of sub-parallel, elongate, north-northeast-trending fissures west of Stevenson Island extending southward toward Dot Island (Figure 3); a series of en echelon, linear, northwest-trending, fissure-controlled, small depressions east and southeast of Stevenson Island; and a downdropped graben north of Stevenson Island, nearly on strike with Lake Village.

Subparallel fissures west of Stevenson Island (Figure 3) plunge as much as 10-20 m into the soft-sediment lake floor 0.5-km southeast of Sand Point. These fissures represent extension fractures whose orientation is controlled by regional north-south structural trends, recognized both north and south of Yellowstone Lake. Active hydrothermal activity is localized along the fissures as shown by dark oxide precipitates partially coating the surfaces of the fissures and shimmering fluids upwelling from these. The fissures, inspected with the submersible ROV for about 160 meters along their NNE trend are narrow (<2 m wide) and cut vertically into soft laminated sediments with no vertical displacement. A parallel set of N-S-trending fissures also occurs 1.3-km northeast of Sand Point. Farther south along this trend, the fissures appear to have well developed hydrothermal vent craters, although investigations with the submersible show only weak or inactive vent fields in the central basin.

Inspection of the features east of Stevenson Island (Figure 3, 6B) using the submersible ROV indicates that small, well-developed hydrothermal vents coalesce along northwest-trending fissures. These may be similar to but more evolved than those to the west of Stevenson Island. The deepest part of Yellowstone Lake, at 133 m, is in the floor of a hydrothermal vent at the south end of the northernmost set of aligned vents; hydrothermal fluids from vents at this location are as hot as 120°C.

Finally, east-west seismic-reflection profiles across the down-dropped block north of Stevenson Island reveal a north-northwest-trending graben structure bounded by normal faults (Kaplinski 1991; Otis and Smith 1977; Shuey et al. 1977). Measured displacements along the two bounding faults vary, but displacement along the western boundary is generally ~6 m whereas that along the eastern normal fault is ~2 m. The eastern bounding fault cuts Holocene lake sediments indicating recent movement. Seismic profiles across the graben project (or strike) toward Lake Village, posing a potential seismic hazard in that area.

All of the above-described sublacustrine structures, the regional tectonic framework of the northern Rocky Mountains, and the still-active cooling sub-caldera magma chamber (Eaton et al. 1975; Fournier 1989; Fournier et al. 1976; Lehman et al. 1982; Stanley et al. 1991; Wicks et al. 1998) play important roles in shaping the morphology of the floor of Yellowstone Lake as revealed in the

bathymetric map, especially of the western part of the northern lake basin. Many of the recently identified features, such as the active fissures west of Stevenson Island and the active graben north of Stevenson Island, are oriented roughly north-south, and may be related to a regional structural feature in western Yellowstone Lake on strike with the Neogene Eagle Bay fault (Figure 1B) (Locke and Meyer 1994; Pierce et al. 1997), perhaps coincident with the inferred margin of the 2.1-Ma Huckleberry Ridge caldera (Christiansen 1984; Christiansen 2001; Hildreth et al. 1984; U.S.G.S. 1972). Seismicity maps of the Yellowstone region (see U.S. Geological Survey Yellowstone Volcano Observatory website: <http://volcanoes.usgs.gov/yvo>) show concentrations of epicenters along linear N-S trends in the northwestern portion of the lake.

Summary and Conclusions

An important outcome of recent studies in Yellowstone Lake is the extension of the subaerial geologic mapping, allowing the lake basin to be understood in the geologic context of the rest of the Yellowstone region (Blank 1974; Christiansen 1974; Christiansen 2001; Richmond 1973; U.S.G.S. 1972). Rhyolitic lava flows contribute greatly to the geology and morphology of Yellowstone Lake. We infer from our high-resolution bathymetry and aeromagnetic data that Stevenson, Dot, and Frank Islands are underlain by a large-volume rhyolitic lava flows (Figure 3). Mapped late Pleistocene glaciolacustrine sediment deposits on these islands merely mantle or blanket the flows (Otis and Smith 1977; Richmond 1974; Richmond and Waldrop 1975; Shuey et al. 1977). Similarly, the hydrothermally cemented beach deposits exposed on Pelican Roost (Figure 3), located ~1 km southwest of Steamboat Point (Figure 3), may also blanket a submerged large-volume rhyolite flow. The margin of the Yellowstone caldera (Otis and Smith 1977; Richmond 1974; Richmond and Waldrop 1975; Shuey et al. 1977) passes through the central part of the lake and northward along the lake's eastern edge (Figure 1). Similar to most of the rest of the margin of the Yellowstone caldera (Figure 1A), we suggest that postcaldera rhyolitic lava flows are present along much of the caldera margin beneath Yellowstone Lake.

Additional and significant potential hazards inferred from the bathymetric, seismic, and submersible surveys of Yellowstone Lake include the effects of potential hydrothermal explosions and related phenomena, such as the ejection of debris, landsliding along the lake margins, and sudden collapse of the lake floor through fragmentation of hydrothermally altered cap rocks. Any of these events could result in a sudden and dramatic shift in lake level, generating a small tsunami that could cause catastrophic local flooding. Ejecta from past hydrothermal explosions that formed craters in the floor of Yellowstone Lake extend several kilometers from their crater rims and include rock fragments in excess of several meters in diameter (Hamilton 1987; Love and Good in press; Morgan et al. 1998; Richmond 1973; Richmond 1974; Richmond 1976; Richmond 1977). In addition to potential hazards to humans, such explosions are likely to be associated with the rapid release into the lake of steam and hot water (Fournier et al. 1991), possibly affecting water chemistry by the release of potentially toxic trace

metals. Such changes could be significant to the fragile ecosystem of Yellowstone Lake and vicinity (Shanks et al. 2001).

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Documenting Trends in Yellowstone's Beaver Population: A Comparison of Aerial and Ground Surveys in the Yellowstone Lake Basin

Sue Consolo Murphy and Douglas W. Smith

Introduction

The beaver (*Castor canadensis*) is a keystone species that can affect ecosystem structure and dynamics beyond its own immediate requirements for food and space (Novak 1987) and thus may be of particular interest to researchers and managers of wildland ecosystems. This species is sometimes erroneously portrayed as missing from Yellowstone National Park, but the historical record contradicts this. Although there has been relatively little research or monitoring of beaver during the park's nearly 130-year history, earlier records (Warren 1926; Jonas 1955; Fullerton 1980; Houston 1982) provide information on beaver activity and distribution from the early 1900s until the 1980s (Consolo Murphy and Hanson 1993).

In 1988–1989, the senior author initiated a sampling survey to document the presence and distribution of beaver in the park and develop a monitoring scheme to assess changes in the status of the species over time. This was a ground survey similar to that most recently undertaken by Fullerton in 1979–1980 (Fullerton 1980). Beavers typically, but not always, construct large lodges built of sticks and mud, anchored most often on the banks of a lake or river, particularly on river bends where the water deepens or at the confluence of two streams. Beavers sometimes use dens in river banks rather than (or in addition to) constructed lodges. Beavers also cut woody vegetation, which is often consolidated and stored in a floating mat, called a cache, anchored to a lodge or located on the water surface near where a beaver colony winters (Jenkins and Busher 1979; Novak 1987). Lodges augmented with freshly cut trees and stems with stripped branches or newly placed mud, new food caches, bank dens, fresh slides down a bank, and recently built dams are also signs of current beaver activity easily observed in autumn, as the animals are then at the height of activity constructing lodges, repairing dams, and caching food for the winter.

Ground surveys were completed by one or two persons who hiked to lakes and along suitable riparian corridors of the park, recording signs of current beaver activity, including lodges, food caches, dams, bank dens, felled trees, stripped stems, beaver trails, and canals. Biologists recommended that beaver surveys be repeated at five-year intervals to build a database on trends in the number and distribution of colonies over time (Consolo Murphy and Hanson 1993), and the senior author and her field assistants did repeat the survey as planned in 1994 (Consolo Murphy and Tatum 1994).

In 1996, Doug Smith, a newly arrived park biologist, was able to obtain funds to conduct the park's first near-complete autumn aerial count of beaver colonies with food caches (Smith et al. 1997). His method was to survey watercourses, ponds, and lakes of suitable gradient from a fixed-wing Supercub plane, flying at an altitude of 100 to 175 feet at an air speed of 55 to 65 mph (Hay 1958; Payne 1981), a widely used survey technique. Every river system in the park was surveyed once, and repeat overflights were often used to census beaver colonies in high-density habitats. Lodges and food caches are easily visible in the fall from slow-flying aircraft after deciduous plants have shed their leaves and before snow and ice form on water surfaces. Smith repeated this survey in 1998 and recommended continuation of aerial surveys at two- to three-year intervals to monitor beaver distribution in the park (Smith 1998).

Since a third iteration of the ground survey was due to be completed in 1999, the park biologists with previous experience surveying beaver decided to compare efforts and techniques in order to build a long-term, affordable monitoring strategy for this species in the park. Some studies have found ground surveys to be more accurate in finding and censusing beaver in non-mountainous terrain, and this may be so in the park as well (Robel and Fox 1992), but they may be prohibitively costly in survey time and dollars. Aerial surveys of late-season food caches are easily conducted and cost-effective (Swensen et al. 1983; Robel and Fox 1992) but are not believed to document the presence of all bank-denning beaver nor those associated with an atypical cache pattern. We compared the effectiveness of the two methods by conducting both a ground survey and an aerial survey in the autumn of 1999 in an area of high-density beaver occupation: along the upper Yellowstone River from the southern park boundary to Yellowstone Lake.

Study Area

The Yellowstone River and its tributaries drain the eastern half of the park. The Yellowstone flows into the southeastern portion of the park (the Thorofare region) and meanders north-northwest for about 26 km (16 mi) to Yellowstone Lake along a mostly flat gradient. The inlet to Yellowstone Lake is a large, marshy delta that supports extensive tall willow communities (*Salix* spp.). Previous ground and aerial surveys have shown that several dozen beaver colonies are generally located in this corridor. Smith (1998) calculated the density of beaver colonies here as 0.35 per km (1.5 per 2 mi) of river surveyed, one of the two highest-density areas of occupation across Yellowstone National Park (the other being an 8.6-km stretch of the Madison River). The survey area included an estimated 9.54 km of streambank and lakeshore in the Yellowstone River delta, 1.97 km in nearby sloughs or ponds, and 19.25 km of streambank upriver along the Yellowstone and the lower reaches of its tributaries (Figure 1), for a total of 30.77 km.

Results

The ground survey of this study area was conducted on three days: September

14 and October 2–3, 1999. On September 14, two ground crews of two persons each initiated the survey from Trail Creek at the tip of Yellowstone Lake's Southeast Arm. One crew (including the senior author) departed via canoe, crossed the arm, and proceeded up the Yellowstone River for approximately 3.2 km, beyond which the upstream current of the river precluded progress. At a number of spots, the crew beached the canoe and searched from the ground, hiking through the dense willow patches. The second crew surveyed on foot between Trail Creek and the Yellowstone River upstream from the delta; initial plans to proceed all the way upriver to the park boundary at Thorofare were delayed due to an injury suffered by one member of this ground crew. Another two-person team thus completed the survey upstream of Cabin Creek in early October. Ground survey crews located a total of 17 active colonies: 13 lodges with food caches, two bank dens with food caches, and two lodges with freshly cut stems, mud, or other signs of current activity but no obvious food cache present (Figure 1). Ten of the colonies were within the Yellowstone River–Beaverdam

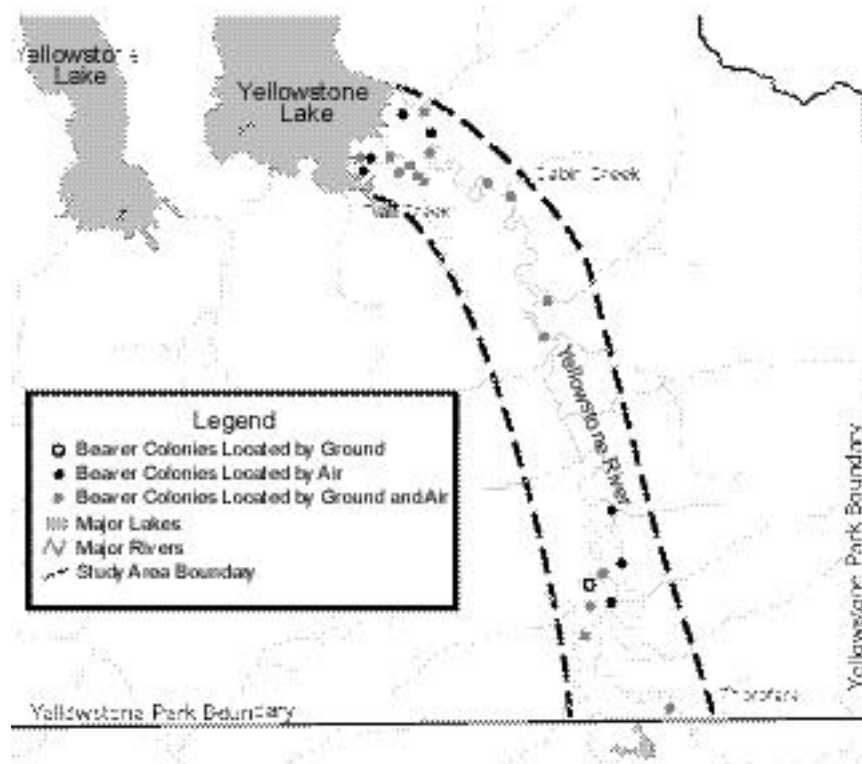


Figure 1. Study area from Yellowstone Lake upstream along the Yellowstone River to the park's southern boundary, and active beaver colonies found by ground survey, aerial survey, and both methods in September–October 1999.

Creek delta area, and seven were upstream of Cabin Creek. The ground survey took eight 10-hour person-days, since safety concerns compelled us to pair observers traveling in the backcountry by either foot or canoe. Total cost was \$1,270 in personnel; equipment was already available for general park purposes.

The aerial survey was conducted on October 25, 1999, by one observer (the junior author) in addition to the contract pilot, flying in a Supercub at an average speed of 55–65 mph from 100 to 175 feet above the river and its main tributaries between the delta and the park boundary. (It was part of a parkwide survey flight.) They observed a total of 23 active beaver colonies in the study area. All of the aerial observations were of lodges or bank dens with caches; 14 of the colonies were within the delta and nine were upstream of Cabin Creek (Figure 1). The aerial survey took 1.5 hours of flight time at a cost of \$115 per hour plus the salary of the park biologist observer, for a total cost of \$212.

Comparison of Techniques

The ground and air observers co-located 16 active colonies: one was located only by the ground crew and seven were located only by the aerial observers, for a total of 24 colonies active within the study area in autumn of 1999. Using a capture/recapture double-count model, the probability of detecting an active colony was 94% by aerial survey and 69% by ground survey. The lower level of detection by ground observers was due to several reasons, none of which were unexpected, especially in this area. All the beaver colonies within the study area were associated with willow communities. The large expanse of flat, marshy habitat present in the Yellowstone River delta is extremely challenging to survey effectively from the ground. The tall willows block visibility and impede safe passage. Even upriver along the Yellowstone, there are extensive willow habitats that are time-intensive and risky to survey; crews were ever alert to the possibility of encountering moose or bears, particularly, in the thick vegetative cover. Also, scattered across the delta are small streams, backwaters, and ponds that are difficult to visit in an efficient manner; it is ideal country to survey from aircraft.

All four of the colonies not seen by ground observers within the delta were some distance from the shore of Yellowstone Lake or the main course of the Yellowstone River, in areas not effectively covered by ground crews. Of note, although two of the colonies within the delta called “active” by ground crews were not recorded as having food caches on September 14, they were recorded as having both an active lodge and cache during the aerial survey. This could be a result of the beavers not having yet begun to actively cache food in mid-September, or because caches are not always visible to ground crews, depending on how closely they can see a lodge; crews tried not to approach too closely lest beavers be disturbed during the survey.

Upstream from the delta, three colonies along the Yellowstone River were seen from the air but not by ground crews, due to the latter having exhausted their ability to cover the area effectively within a reasonable period of time. One colony observed from the air, near the confluence of the north fork of Cliff Creek and the Yellowstone River, was in an area noted by ground observers to have an

abundance of sign but no evident lodge or cache; ground crews may have missed it, or it may have been constructed after the ground survey occurred. The one colony found by ground observers but not seen from the air was a lodge near the river's confluence with the south fork of Escarpment Creek. Ground observers described the lodge as concealed within early-season flood debris. It had no food cache anchored to it, though a very large one was just upstream around the next river bend; during the October 3 survey the ground crew did observe a large beaver swimming between the two sites. This points out one of the situations where ground surveys may be more effective at finding beaver colonies that are hard to see from the air. Another situation that occurs in the park, but not in this study area, is one in which beaver colonies occupy less-typical habitats—particularly streams or lakes without willows, aspens, or cottonwoods. In these settings, such as ground crews observed at Heart Lake in 1999, beavers may rely on other foods such as pond lilies (*Nuphar polysepalum*) or submerged aquatic plants. A food cache, if present, may not be visible from the air.

Summary

Aerial surveys should not be construed as providing a complete count of beaver lodges and caches. However, the results of this survey indicate that, for most park purposes, aerial surveys have a high probability of detecting active beaver colonies in the autumn when beaver are most active and likely preparing to overwinter in the observed location. In comparison, a yearly ground survey is more costly and, at least in difficult-to-survey terrain, less likely to document as high a percentage of the existing beaver colonies (Table 1). In general, we find that aerial surveys are a cost-effective method to survey for trends in the number and distribution of beaver colonies that exist across Yellowstone National Park. Since the park's current budget and work plans call for biennial beaver survey flights, periodic ground surveys can help test the efficiency of flights to monitor colonies, especially in marginal or atypical beaver habitats. Ground survey data may augment the data from aerial counts, especially in areas where beavers are likely to bank-den or overwinter without building visible food caches. Ground surveys also permit observers to better view animal behavior and appreciate the

Table 1. A comparison of ground and aerial survey costs and results from the 1999 study.

Results Compared	Ground survey	Aerial survey
Number of beaver colonies found	17	23
Number not found by other method	1	7
Detection probability	17 of 24 (69%)	23 of 24 (94%)
Time required (10-hr person-days)	8.0	0.188
Cost of survey	\$1,270	\$212 w/o ferry time

extent of beaver cutting, construction, and habitat alteration that occurs in specific sites as a result of the animal's periodic presence and withdrawal. Since Yellowstone lacks data on relationships between the numbers of active lodges or food caches and the beaver population, we suggest that further research to estimate the average size of the beaver colonies in various park habitats would be of benefit to resource managers, interpreters, and others.

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